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Neogene Paleontology in the Northern
Dominican Republic

21. The Genus *Prunum* (Gastropoda: Marginellidae)

by

Ross H. Nehm

22. The Family Neritidae (Mollusca: Gastropoda)

by

Fábio H. A. Costa, Ross H. Nehm, and Carole S. Hickman

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Ross H. Nehm

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NEOGENE PALEONTOLOGY IN THE NORTHERN DOMINICAN REPUBLIC 21.
THE GENUS *PRUNUM* (GASTROPODA: MARGINELLIDAE)

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ABSTRACT

Marginellid gastropods are a prominent and well-preserved element in five well-studied and sampled Neogene stratigraphic sections of the Cibao Valley of the northern Dominican Republic. Among the marginellids, species of the genus *Prunum* (Hermannsen, 1852) are the most abundant, diverse, and temporally wide-ranging in these sections. Seven species (of which two are new) occur in these sections. They are: *P. aminum* (Dall, 1896); *P. christineladde* (Maury, 1917a); *P. conforme* (Sowerby, 1850); *P. latissimum* (Dall, 1896); *P. maoense* (Maury, 1917a); *P. mauryense* n. sp.; and *P. gibsonsmithorum* n. sp. Detailed analyses of the biostratigraphy, paleoecology, biogeography, and ontogenetic and spatiotemporal morphologic variation are presented for these species.

Prunum aminum is rare and occurs in the Baitoa Formation of the Río Yaque del Norte at López. *Prunum christineladde* occurs abundantly in the upper Gurabo Formation of the Río Gurabo, and in the lower Mao Formation of the Cañada Zalaya. *Prunum christineladde* is restricted to deep marine (>150 m depth) paleoenvironments. Morphometric analyses indicate that *P. christineladde* becomes significantly smaller and proportionally narrower through time in the Río Gurabo section. *Prunum conforme* is the most widespread species (geographically and temporally) and occurs rarely in the Baitoa Formation of the Río Yaque del Norte and the Cercado Formation of the Río Mao. In contrast, *P. conforme* occurs abundantly in the Gurabo Formation of the Río Cana, the Gurabo Formation of the Río Gurabo, and the Mao Formation of the Cañada Zalaya. *Prunum conforme* occurs in shallow to deep marine paleoenvironments (40–200 m depth). Morphometric analyses of shell size and shape in the Río Gurabo and Río Cana sections indicate that no net morphological change occurs through time in *P. conforme*, but geographic differences occur between samples from the middle Gurabo Formation of the Río Gurabo and the Río Yaque del Norte section. *Prunum gibsonsmithorum* is rare and occurs in the Gurabo Formation of the Río Cana. *Prunum latissimum* is the most abundant Dominican *Prunum* species (>700 specimens) but is restricted to the Baitoa Formation of the Río Yaque del Norte. *Prunum latissimum* occurs in sediments deposited in shallow (<30 m depth) high-energy environments. Analyses of shell size and shape through the López section at Baitoa indicate that, despite pronounced morphological oscillations in size and shape through time, no net morphological change and no directional anagenetic change occur in *P. latissimum*. *Prunum maoense* is the second most abundant Dominican species and occurs in the Cercado and Gurabo Formations of the Río Cana and Río Gurabo, and the Cercado Formation of the Río Mao. *Prunum maoense* occurs in sands and silts deposited in shallow marine environments (0–40 m depth) and is associated with the seagrass epibiont *Smaragdia*. Analyses of shell size and shape through the Río Cana and Río Gurabo sections indicate that no net morphological change occurs in *P. maoense*. *Prunum mauryense* occurs abundantly in one sample (TU 1227A) from the Mao Formation of the Cañada Zalaya.

Six morphological features are used to distinguish juvenile and adult shells and to analyze ontogenetic variation within and among species. These features are: (1) An aperture margin callus; (2) Lip denticulations and/or crenulations; (3) Inner lip thickening; (4) A terminal inflection of the body whorl; (5) the external varix; and (6) a posterior lip callus. Dominican *Prunum* species share several patterns of ontogenetic change. In all species, shouldering and aperture area decrease through ontogeny whereas spire height increases through ontogeny. All species exhibit: (1) four columellar plications throughout ontogeny; (2) a plication callus in early ontogeny; and (3) an aperture margin callus in late ontogeny. Lastly, in all species inner lip thickening occurs before the formation of the external varix. Through ontogeny, Dominican *Prunum* differ in a number of traits: (1) the magnitude of aperture margin callus; (2) spatial patterns of callus expansion from the area of the columellar plications; and (3) the presence and location of callus processes. These three features are significant because they influence the shape and area of the aperture. In general, the early ontogenetic stages of Dominican *Prunum* (whorls one and two) are very similar whereas the late ontogenetic stages (whorls three and four) are very different. Adult *P. christineladde*, however, are very similar to late-stage juveniles of *P. conforme*, and adult *P. maoense* are very similar to late-stage juveniles of *P. latissimum*.

Biogeographically, half of Dominican *Prunum* species are endemic (*P. christineladde*, *P. mauryense*, *P. gibsonsmithorum*, and *P. aminum*). High levels of endemism are expected in marginellids because all living and fossil *Prunum* species are nonplanktotrophic and living species have geographically restricted ranges. This endemism in Dominican *Prunum* is similar to that observed in many other Dominican mollusk clades.

RESUMEN

Los gastropodos marginelidos son elementos importantes y bien preservados de los sedimentos de el periodo Neogeno en el Valle de Cibao en el Norte de la República Dominicana. Entre los Marginelidos, especies de el genero *Prunum* (Hermannsen, 1852) son los mas abundantes, su rango varía de manera temporal, frecuentemente en cinco secciones estratograficas que han sido extensamente estudiadas. Siete especies, dos nuevas, se encuentran en estas secciones, las cuales son: *Prunum aminum* (Dall, 1896); *P. christineladde* (Maury, 1917a); *P. conforme* (Sowerby, 1850); *P. latissimum* (Dall, 1896); *P. maoense* (Maury, 1917a);

P. mauryense n. sp.; and *P. gibsonsmithorum*, n. sp. Análisis detallados de la esteratigrafía biológica, paleoecología, variación ontogenética, y la variación en espacio y tiempo en la morfología de estos organismos, son presentadas para las especies mas abundantes.

Prunum aminum es rara en la Formación Baitoa de el Río Yaque de el Norte en López. *Prunum christineladdeae* es abundantemente y se encuentra en la Formación superior de el Río Gurabo, y en la Formación inferior de la bocana de el Río de la Cañada de Zalaya. *Prunum christineladdeae* es restringida a las profundidades marinas y medios (>150 m) ambientes paleontológicos. La análisis morfométricos indican que *P. christineladdeae* se modifica al paso de el tiempo haciendose significativamente mas pequeña y delgada en esta sección de el Río Gurabo. *Prunum conforme* es la especie que esta mas ampliamente distribuida tanto temporal como geográficamente y aparece raramente en la Formación Baitoa de el Río Yaque de el Norte y la Formación de Cercado en la bocana de el Río Mao. *Prunum conforme* se encuentra de una manera abundante en La Formación Gurabo de el Río Cana, la Formación de Gurabo de el Río Gurabo, y La Formación Mao de la Cañada de Zalaya. *Prunum conforme* se encuentra en paleoambientes marinos tanto poco profundos, así como profundos. El análisis morfométrico de el tamaño de la concha así como de su forma en las secciones de el Río Gurabo y en el Ríos Cana indican que no hay un cambio neto significativo a través de el tiempo en *P. conforme*, pero hay diferencias geograficas entre las muestras. *Prunum gibsonsmithorum*, raramente ocurre en la Formación Gurabo de el Río Cana. *Prunum latissimum* es la especie de mas abundante (> 700 individuos) en la República Dominicana y se encuentra restringida a la Formación Baitoa de el Río Yaque de el Norte. *Prunum latissimum* se puede encontrar en sedimentos probablemente poco profundos y con alta energía (<30 m). El análisis de el tamaño y la forma de las conchas a través de la sección López en Baitoa indica que no hay un cambio morfológico neto y no hay una dirección en el cambio genético que ocurra en *P. latissimum*. *Prunum maoense* es la segunda especie mas abundante en la República Dominicana y ocurre en las Formaciones de Cercado y Gurabo de el Río Cana y Río Gurabo, y en la Formación Cercado de el Río Mao. *Prunum maoense* se encuentra en arenas y arcillas que en aguas bajas y estuarinas. Análisis de el tamaño y la forma de las conchas a través de la sección de el Río Cana y Gurabo indican que no hay un cambio morfológico neto. *Prunum mauryense* se encuentra abundantemente en una de las muestras de la Formación Mao de la bocana de la Cañada de Zalaya.

Seis características morfológicas han sido usadas para distinguir conchas de juveniles y adultos y para analizar la variación ontogenética dentro y entre especies. Estas características son: (1) La abertura de el margen de el callo; (2) Las denticulaciones y craneaciones de el labio; (3) El grueso de el labio interior; (4) El doblez terminal de la espiral superior de la concha; (5) La parte externa de el "varix;" (6) El callo posterior de el labio. Las cuatro especies de *Prunum* comparten las siguientes características a través de su ontogenia; el alto de la espiral se incrementa, el area de la abertura se reduce, la parte superior de el hombro de la concha se reduce tambien, tienen cuatro dobleces en la columnela. A través de la ontogenia las especies Dominicanas se diferencian en lo siguiente: el contenido de callo, su forma y la presencia de los procesos en los callos. Los primeros estados ontogenéticos comparten la mayoría de las similitudes morfológicas mientras que los últimos estados ontogenéticos comparten la mayoría de las diferencias.

Biogeográficamente más de la mitad de los *Prunum* en la República Dominicana son endémicos (*P. aminum*, *P. christineladdeae*, *P. mauryense* n. sp., and *P. gibsonsmithorum*, n. sp.). Un alto porcentaje de especies endémicas es de esperarse porque todas las especies fociles y vivientes son nonoplantotróficas y las especies vivientes tienen rangos restringidos. El gran porcentaje de especies endémicas es similar a muchos otros de los lineages de molluscos en la República Dominicana.

INTRODUCTION

This paper is a contribution to the Dominican Republic Research Project, an ongoing multidisciplinary research program designed to investigate the geological, paleoecological, and evolutionary changes in the rich Neogene fossil fauna of the northern Dominican Republic. The first phase of the project, begun in the late 1970s, involved field survey, collection of fossil material, and the study of the lithology, stratigraphy, and age of the sediments of the Yaque Group of the Cibao Valley (Saunders *et al.*, 1986). The second phase is ongoing, and encompasses several research agendas: (1) The detailed systematic and biostratigraphic study of Dominican fossil groups (for example, Jung, 1986, 1994, 1996; Jung and Petit, 1990; Budd, 1987; Budd *et al.*, 1994; van den Bold, 1988; E. Vokes, 1989; H. Vokes, 1989; Anderson, 1996); (2) Investigation of the tempo and mode of evolutionary change in Dominican species (Cheetham, 1986, 1987; Nehm and Geary, 1994; Anderson, 1994; Nehm, 1998, in press); and (3) Patterns of faunal distribution and evolutionary turnover in Dominican and other Carib-

bean faunas (Anderson *et al.*, 1992; Jackson *et al.*, 1993; Budd *et al.*, 1994, 1996). The integration of these research agendas has the potential to produce a comprehensive understanding of the geological, paleoenvironmental, and paleoecological context of macroevolutionary change within and among invertebrate clades and communities.

Marginellid gastropods are a prominent and well-preserved element of the Neogene fossil fauna of the Dominican Republic. Five marginellid genera, *Dentimargo*, *Eratoidea*, *Marginella*, *Volvarina* and *Prunum*, are represented in these deposits. *Prunum* is the most diverse and abundant marginellid clade in the Yaque Group deposits; approximately 2,000 specimens of seven *Prunum* species occur in the NMB and TU collections from the Baitoa Formation (Lower to Middle Miocene) to the Mao Formation (Lower Pliocene), over an interval of at least 11 million years. *Prunum* is an excellent system for morphological research because the shell preserves a nearly complete record of ontogeny (visible using x-radiography and hard-tissue histology) and morphological features that mark the

termination of growth at sexual maturity, thus permitting the distinction between juvenile and adult shells. *Prunum* species are ecologically diverse in these deposits and occur in brackish, shallow marine, and deep-marine paleoenvironments. *Prunum* shells are taphonomically durable and well-preserved in the Dominican stratigraphic sections because of their thick and extensively callused body whorl and varix-reinforced lip. Intricate color patterns, which are important species-diagnostic characters, are preserved in most Dominican fossil marginellid genera (e.g., *Prunum*, *Marginella*, and *Eratoidea*). These morphological attributes, in addition to their ecological diversity, good preservation, and numerical abundance, make *Prunum* a particularly appropriate group for examining ecological and evolutionary patterns within and among taxa in the Dominican Republic and throughout the Caribbean Basin (e.g., Nehm, 1998).

The Upper Miocene to Lower Pliocene stratigraphic sections in the Cibao Valley precede a crucial period of evolutionary change in the western Atlantic invertebrate biota. Large-scale faunal-level studies suggest that the Upper Pliocene was a time of considerable extinction and speciation of western Atlantic mollusks (Jackson *et al.*, 1993; Allmon *et al.*, 1993). The timing, magnitude, and causes of these changes are still poorly understood, and few studies of extinction and speciation patterns in Caribbean clades have been completed. The Dominican Republic sections are therefore important because they contribute to an understanding of the faunal composition of the region prior to the Pliocene turnover event. The study of individual clades from these sections is also necessary in order to document, analyze, and understand biodiversity dynamics in the Caribbean Neogene precisely (e.g., Jackson *et al.*, 1996).

Dominican *Prunum* species figure prominently in a larger study of the phylogeny and macroevolutionary patterns in western Atlantic and eastern Pacific *Prunum* (Nehm, 1998, in press). This study provides the necessary but often ignored biostratigraphic, paleoecologic, morphologic, and systematic framework for future micro and macroevolutionary studies employing Dominican *Prunum* species. Specifically, herein *Prunum* species are placed in a modern systematic framework, the temporal and geographic distributions of fossil species are refined, and morphologic and ontogenetic variation is studied in relation to paleoenvironmental gradients. Ultimately, this information will be synthesized with data from ongoing studies of *Prunum* from Venezuela, Central America, Mexico, and the Atlantic Coastal Plain in order to examine clade-level patterns of evolution and extinction within the region, and to compare evolutionary patterns within marginellid clades to faunal-level patterns of evolutionary turnover.

nellid clades to faunal-level patterns of evolutionary turnover.

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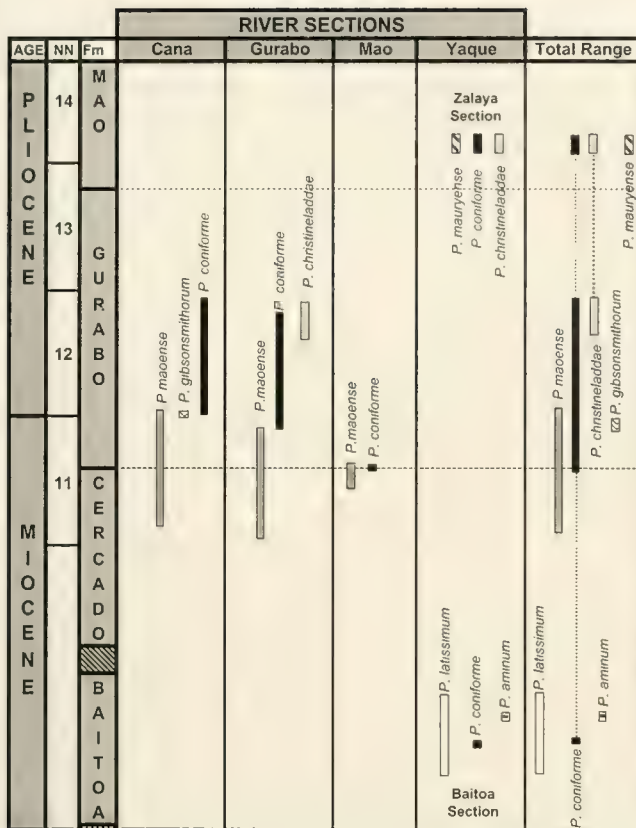
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ABBREVIATIONS OF REPOSITORY INSTITUTIONS

- NMB: Naturhistorisches Museum Basel, Switzerland.
- PRI: Paleontological Research Institution, Ithaca, New York, U.S.A.
- TU: Tulane University, New Orleans, LA, U.S.A. (material now housed at PRI).
- UCMP: University of California Museum of Paleontology, Berkeley, CA, U.S.A.
- USNM: U.S. National Museum of Natural History, Washington, DC, U.S.A. (Five digit catalog numbers refer to the Department of Invertebrate Zoology, six-digit catalog numbers refer to the Department of Paleobiology).

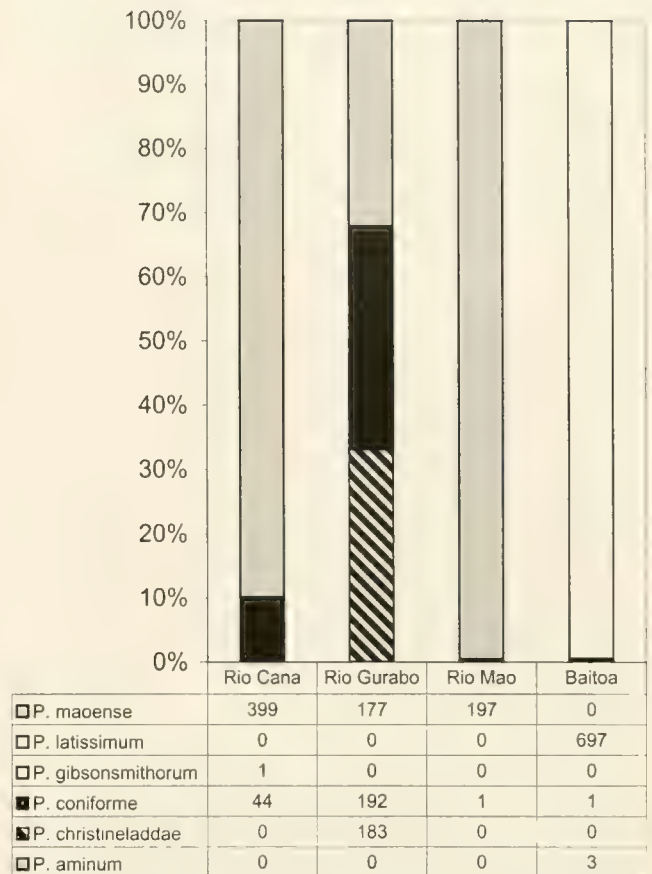
STRATIGRAPHIC DISTRIBUTION

Seven species of the marginellid genus *Prunum* occur in the Neogene sediments of the Yaque Group of the Cibao Valley. They are: *P. aminum* (Dall, 1896); *P. christineladdae* (Maury, 1917); *P. coniforme* (Sow-



Text-figure 2.—Stratigraphic distributions of Dominican species of *Prunum* from the Yaque Group of the Cibao Valley. River sections are labeled at the top (from west to east). Neogene Nannofossil (NN) zones are listed at the left and correlated with the Cercado, Gurabo, and Mao Formations. The Baitoa Formation has not been dated using planktonic foraminifera, but it is thought to be of Early or Middle Miocene age based on biostratigraphic data from ostracods and molluscs (Saunders *et al.* [1986] and Vokes [1979]). See Text-figure 1 for geographic locations of the River sections. Stratigraphic and biostratigraphic information from Saunders *et al.* (1986).

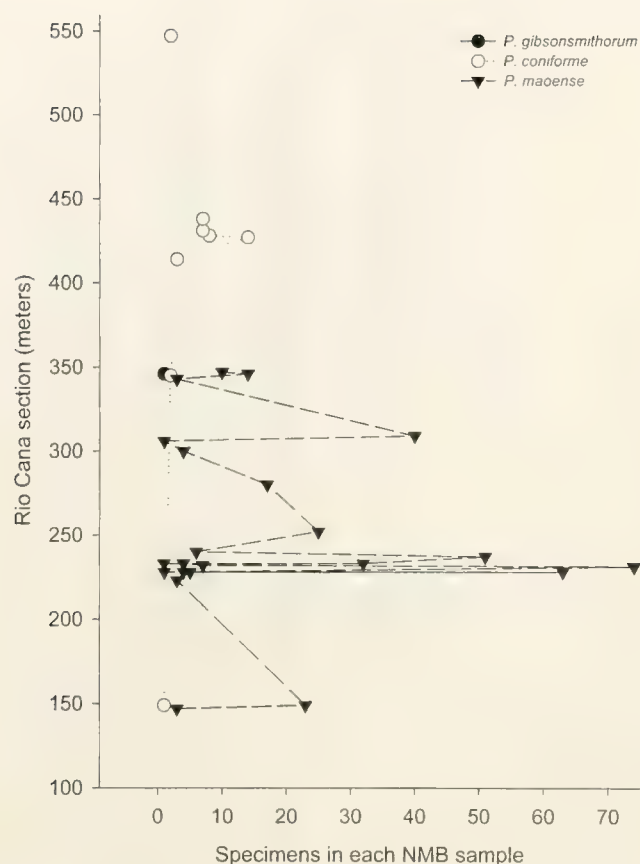
contain *Prunum maoense*, *P. conforme* and *P. gibsonsmithorum*. *Prunum maoense* is the most abundant species in the section (399 specimens), and occurs in 24 NMB samples. It first appears at NMB 17005 at approximately 147 m in the lower Cercado Formation and last occurs at NMB 16818 at approximately 347 m in the lower Gurabo Formation. *Prunum maoense* is most abundant between 215 and 230 meters in the Río Cana section. *Prunum conforme*, the second most abundant species in the section (44 specimens), occurs in eight NMB samples. It first occurs at NMB 16857 from about 149 m in the Cercado Formation and last occurs at NMB 16869 at about 547 m in the upper Gurabo Formation. *Prunum gibsonsmithorum* is rare: one specimen was collected in NMB 16818 near 347 m in the section and one specimen was collected at TU 1354. Although the stratigraphic ranges of these



Text-figure 3.—Relative abundances of *P. aminum*, *P. christineladdae*, *P. conforme*, *P. gibsonsmithorum*, *P. latissimum*, and *P. maoense* in the Río Yaque del Norte (López), Río Mao, Río Gurabo, and Río Cana stratigraphic sections. See Text-figure 1 for the geographic locations of river sections.

three species overlap slightly, nearly all samples containing *P. maoense* occur low in the section, whereas most samples containing *P. conforme* occur high in the section. This pattern is also apparent in the Río Gurabo section (see below).

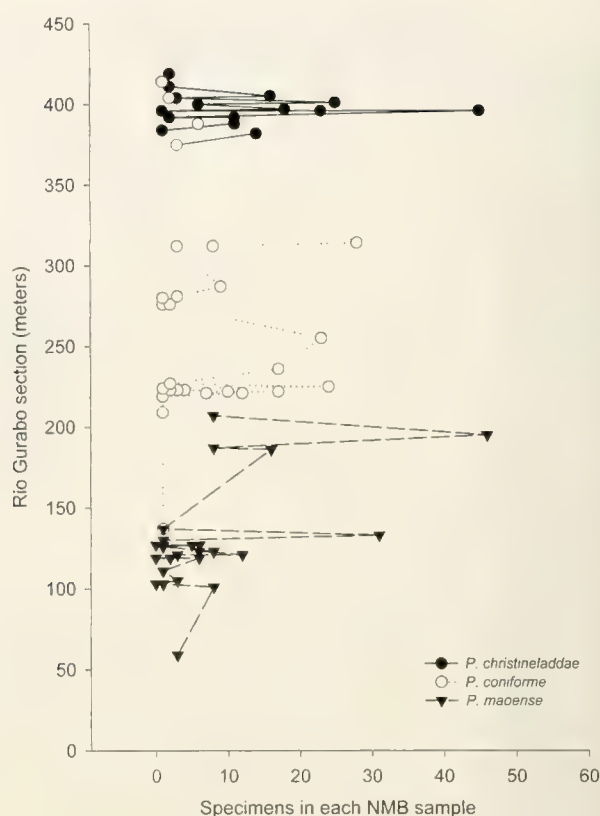
Río Gurabo (see Text-fig. 5).—Sixty-eight NMB samples from the Río Gurabo section contain approximately 550 specimens of *Prunum conforme*, *P. christineladdae*, and *P. maoense*. As in the Río Cana section, *P. maoense* occurs lower in the Río Gurabo section than the other *Prunum* species. It is the least abundant *Prunum* species in the section (177 specimens) and occurs in 25 NMB samples. *Prunum maoense* first occurs at NMB 15919 at about 59 m in the lower Cercado Formation and last occurs at NMB 15873 at about 207 m in the lower Gurabo Formation. *Prunum maoense* is most abundant near 200 m in the section. The greatest number of samples containing *P. maoense* occur from 100 to 140 meters in the section. *Prunum conforme* is the most abundant *Prunum* species in the



Text-figure 4.—Stratigraphic distributions of NMB samples containing *Prunum* species, and the number of specimens in each sample, in the Río Cana section. Samples represent a collection of specimens from a stratigraphically defined position (see Saunders *et al.* [1986], pp. 41–64).

Río Gurabo section (197 specimens) and occurs in 27 samples. It first appears at NMB 15897 at about 137 m in the lower Gurabo Formation, and last appears at NMB 15819 at about 414 m in the Gurabo Formation. *Prunum christineladae* occurs in 16 samples (183 specimens). It first occurs at NMB 15837 near 375 m in the Gurabo Formation and last occurs at NMB 15820 at about 419 m in the upper Gurabo Formation. It is most abundant near 395 m in the section. A series of stratigraphic and morphologic intermediates link *P. conforme* and *P. christineladae* in the upper Gurabo Formation (Nehm and Geary, 1994). As in the Río Cana, the ranges of *P. conforme* and *P. maoense* overlap slightly but nearly all samples containing *P. maoense* occur low in the section, whereas most samples containing *P. conforme* occur high in the section. These species provide useful data for stratigraphic and/or paleoenvironmental correlations between the Río Cana and Río Gurabo stratigraphic sections.

Río Mao.—The fourteen NMB samples containing



Text-figure 5.—Stratigraphic distributions of NMB samples containing *Prunum* species, and the number of specimens in each sample, from the Río Gurabo section. Samples represent a collection of specimens from a stratigraphically defined position (see Saunders *et al.* [1986], pp. 41–64).

Prunum in the Río Mao section are restricted to three sampling areas: Maury's Bluff One, Two, and Three (see Maury, 1917a; Saunders *et al.*, 1986). The stratigraphic positions of these bluffs are uncertain, but faunal and microfossil evidence suggests the bluffs of the Río Mao should be assigned to the upper Cercado and lower Gurabo Formations (Saunders *et al.*, 1986). In the Río Mao section *P. conforme* is rare (one specimen from NMB 16801) whereas *P. maoense* is abundant (about 200 specimens from 13 samples).

Cañada Zalaya.—The Cañada Zalaya samples are from the Mao Formation. These samples are the stratigraphically youngest samples containing *Prunum* in the Cibao Valley (Saunders *et al.*, 1986). Only TU 1227a from the Cañada Zalaya contains *Prunum* specimens. This sample contains *P. mauryense* (>500 specimens), *P. conforme* (about 100 specimens), and broken specimens of *P. christineladae* (about 20 specimens).

Río Yaque del Norte (see Text-fig. 6).—Nineteen NMB samples containing about 700 *Prunum* specimens were collected from the Baitoa section of the Río

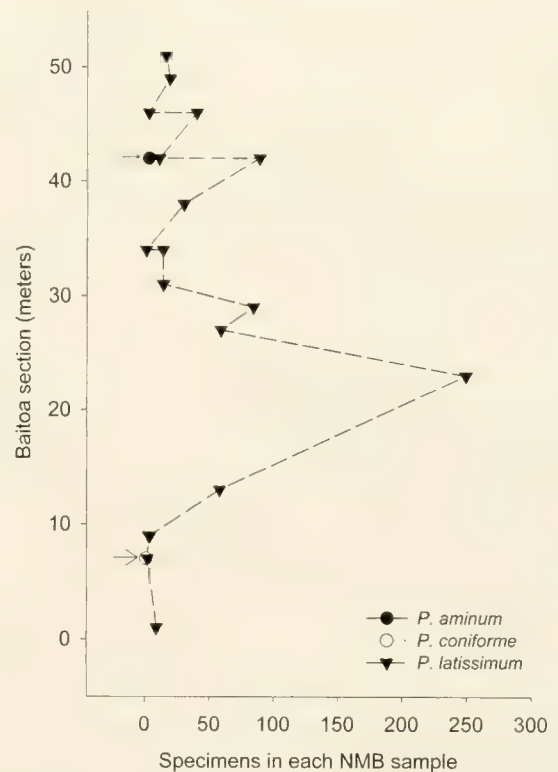
Yaque del Norte. One NMB sample from Arroyo López and one NMB sample from La Barranca also contain *Prunum* specimens. *Prunum conforme* occurs in NMB sample 17275 at Arroyo López (Cercado Formation), and NMB sample 17268 from La Barranca (Gurabo Formation). More detailed information is available on the biostratigraphy of *Prunum* from the Baitoa Formation at López.

The López samples from the Baitoa Formation contain the oldest *Prunum* from the Cibao Valley. The data presented here include the stratigraphic positions of NMB samples above Horizon A, a discordant erosive contact below poorly sorted conglomerates (see Saunders *et al.*, 1986). NMB 17280, about one meter above Horizon A, is the oldest stratigraphic sample in the Dominican Republic containing *Prunum* specimens. *Prunum latissimum* is the most abundant species in the Baitoa section, and the most abundant species in the Dominican Republic Neogene (about 700 specimens from 17 samples). It first occurs at NMB 17280 at about 1 m above Horizon A, and last occurs at NMB 16942, at about 51 m above Horizon A. The abundance of *P. latissimum* peaks at about 25 m in the section, and decreases thereafter. One specimen of *P. conforme* occurs in NMB 17282 at approximately 7 m above Horizon A. *Prunum aminum* occurs at Baitoa in NMB sample 16936 (three specimens at 42 m in the section) and at Arroyo Hondo in TU samples 1363 (two specimens) and 1364 (one specimen).

PALEOECOLOGY

Significant paleoenvironmental and paleoecological differences occur within and among the Neogene sections of the northern Dominican Republic Neogene (Saunders *et al.*, 1986). Paleoenvironments range from brackish to deep marine (>200 m), and include assemblages of seagrass and coral reef associated invertebrates (Nehm and Hickman, 1994; Budd *et al.*, 1996; Costa *et al.*, in press). The relationships of *Prunum* species' first occurrences, last occurrences, and abundances with paleoenvironmental and paleoecological conditions are examined. Paleoenvironmental and paleoecological data from ostracods (Bold, 1988), corals (Budd *et al.*, 1996), foraminifera (Saunders *et al.*, 1986) and mollusks (Saunders *et al.*, 1982; Nehm and Hickman, 1994; Costa *et al.*, in press; Lindberg and Nehm, in prep.) are compared to the distributions and abundances of *P. christineladdae*, *P. conforme*, *P. latissimum*, and *P. maoense*.

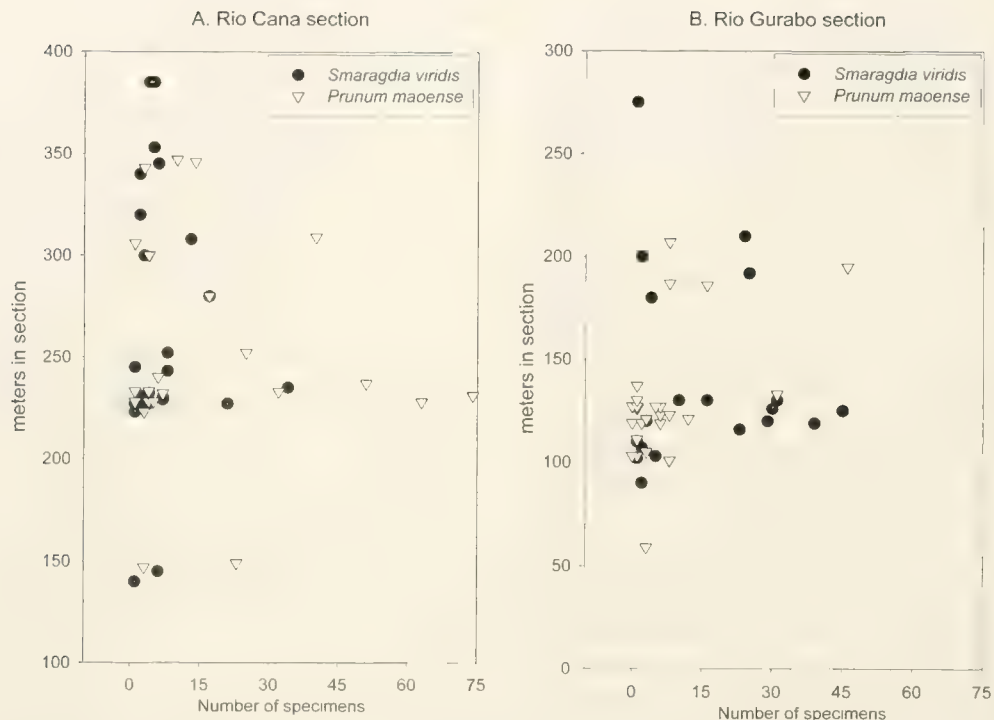
Río Cana.—The Río Cana section contains sediments from brackish, shallow marine, and deep marine environments; progressively offshore and more open marine conditions occur upsection. The distributions of environmentally restricted ostracod species suggest



Text-figure 6.—Stratigraphic distributions of NMB samples containing *Prunum* species, and the number of specimens in each sample, from the Río Yaque del Norte (López) section. Samples represent a collection of specimens from a stratigraphically defined position (see Saunders *et al.* [1986], pp. 41–64).

that brackish-water conditions occur below 150 m and between 200 m and 230 m in the Río Cana section (Bold, 1988). The brackish water *Larkinia-Mytilus-Melongena* mollusk assemblage also occurs in the middle Cercado Formation (Saunders *et al.*, 1982) as do several brackish-water *Anadara patricia* and oyster beds. Sediments of shallow marine origin (<30 m depth) occur from 150 m to 200 m in the section, whereas sediments of deeper marine origin (>30 m depth) occur from 230–450 m in the section (Bold, 1988; Saunders *et al.*, 1986; Anderson, 1996). Paleoecologically, the stratigraphic overlap of grass-flat coral assemblages, seagrass associated limpets, and seagrass associated gastropods (*Smaragdia*) from 230 to 320 m in the Río Cana section strongly suggests that seagrasses were once present in this stratigraphic interval. Coral reefs are well-developed from approximately 340 m to 410 m in the section (Budd *et al.*, 1996).

Prunum maoense first occurs in low abundance (two samples) near 150 m in the section in very shallow marine or brackish deposits (Bold, 1988). No specimens occur from 150 m to 220 m in the section. Subsequently, just above the brackish water *Arca* beds



Text-figure 7.—Stratigraphic distributions and abundances of *Smaragdia viridis* and *P. maoense*. A. Rio Cana section; B. Rio Gurabo section.

(near 220–225 m, Saunders *et al.*, 1986), *P. maoense* is most abundant (in terms of samples and specimens). A second abundance peak occurs near 300 m in the section. Ostracod data suggest progressively offshore and more open marine conditions in this stratigraphic interval. Interestingly, the distribution and abundance of the obligatory seagrass epibiont *Smaragdia viridis* is generally concordant with the distribution and abundance of *P. maoense* in the Rio Cana section (Text-fig. 7A). The last occurrence of *P. maoense* in the Río Cana section occurs near 340 m and coincides with the last occurrence of grass-flat coral communities.

The lower Gurabo Formation contains reef building and branching corals and the first occurrence of planktonic foraminifera (Saunders *et al.*, 1982). This stratigraphic interval contains sediments deposited in clear, low energy environments greater than 30 m depth (Saunders *et al.*, 1986). The stratigraphic interval containing shallow water reefs (340–440 m) overlaps with the stratigraphic range of *Prunum conforme* (Budd *et al.*, 1996). (One specimen of *P. conforme* occurs near 150 m in the Rio Cana section, but no other specimens were collected below 340 m in the section.) The middle Gurabo Formation of the Río Cana contains a deep water interval from 380 m to 420 m in the section where water depths are estimated to be near 100 m (based on the presence of *Cytherella dominica* Bold). This deep water interval contains samples with the

greatest number of *P. conforme* specimens. *P. conforme* last occurs near 555 m in the section, where paleodepths are estimated to be near 150 m (Vokes, 1989).

Río Gurabo.—The Río Gurabo section contains brackish, very shallow marine, shallow marine, and deep marine sediments deposited in progressively offshore and more open marine conditions upsection. The Cercado Formation contains brackish and very shallow marine deposits, whereas the Gurabo Formation contains shallow and deep marine deposits. The brackish water *Larkinia-Mytilus-Melongena* mollusk assemblage, which occurs in the Cercado Formation of the Río Cana, also occurs in the lower Cercado Formation of the Río Gurabo from approximately 20–50 m. Brackish water ostracod species also occur near 50 m in the middle Cercado Formation (Saunders *et al.*, 1986; Bold, 1988). Very shallow marine conditions (<30 m paleodepth) occur from 60–150 m in the section, whereas deeper marine conditions (30 to 100 m paleodepth) occur from 150–380 m in the section.

Prunum maoense first occurs in sand above lignite beds near 56 m in the section. No specimens were collected from a shallow marine interval from about 60–100 m in the section. From about 100–145 m in the section *P. maoense* is most abundant in terms of specimens and samples. This interval also contains seagrass-associated limpets and abundant samples and

specimens of the obligatory seagrass epibiont *Smaragdia*. *Prunum maoense* is also very abundant from about 180 to 210 m in the section, an interval that again contains abundant *Smaragdia* specimens and grass-flat corals (Text-fig. 7B; Budd *et al.*, 1996). This interval of the lower Gurabo Formation contains shallow marine deposits (30–100 m paleodepth) whereas the upper Gurabo Formation contains deep marine deposits (100–200 m paleodepth). *Prunum maoense* last occurs in the lower Gurabo Formation (near 210 m in the section).

Prunum conforme is most abundant in the deeper marine deposits of the lower Gurabo Formation. The first appearance of planktonic foraminifera near 220 m in the section coincides with abundant samples and specimens of *P. conforme* and the last appearance of *Prunum maoense*. The stratigraphic interval containing abundant *P. conforme* also contains reef corals (Budd *et al.*, 1996).

Deposits in the middle Gurabo Formation near the Miocene-Pliocene boundary (380 m) were deposited in depths of 180 m to 200 m (based on the size of *Krithe dolichodeira* and the lack of shallow water ostracod taxa [Bold, 1988]). *Prunum conforme* last appears near 410 m section, where paleodepths are estimated to be greater than 200 m. *Prunum christineladde* occurs abundantly between 380 m and 418 m in the section, during an interval of rapid deepening, an increasingly number of planktonic foraminifera (Saunders *et al.*, 1986), and the last occurrence of abundant reef corals in the Gurabo Formation. A series of stratigraphic and morphologic intermediates between *P. conforme* and *P. christineladde* occur in the deeper water sediments of the Gurabo Formation (Nehm and Geary, 1994).

Río Yaque del Norte at López.—Unlike the Río Cana and Río Gurabo sections, no clear biostratigraphic or paleoecologic patterns are apparent in the López section. Pebbly, well-bedded silts with conglomeratic and coarse sandy layers occur at López. The Baitoa Formation at López contains deposits that appear to be from a much higher energy environment than those of the Cercado and Gurabo Formations of the Río Gurabo and Río Cana (Saunders *et al.*, 1986). Using muricid gastropod ecological data, Vokes (1979) estimated the Baitoa formation to be of shallow marine origin (0–20 m paleodepth). Ostracod data also suggest a shallow water paleoenvironment (Bold, 1988). Additionally, the absence of planktonic foraminifera and calcareous nannofossils in the first 20 m of the section suggests very shallow marine paleoenvironments (Saunders *et al.*, 1982). The remaining 34 m of the section are more finely grained and contain frequent horizons with pebbles and cobbles. Abundant mytilids

suggest lagoonal conditions near 15–20 m in the section (Saunders *et al.*, 1982). *Prunum latissimum* occurs abundantly throughout the section at López, although abundance peaks near 25 m. In contrast, *P. conforme* and *P. aminum* are rare in the López section. The abundance of *Smaragdia* (Costa *et al.*, in press), and the presence of soritid foraminifera (Saunders *et al.*, 1986) indicate that seagrasses were once present in the Baitoa Formation.

The study of the stratigraphic distributions and abundances of *Prunum* species within the Río Cana, Río Gurabo, and López sections and their relationships to paleoenvironmental and paleoecological conditions provides information on the paleoecological preferences of *Prunum* species within the Neogene sediments of the Cibao Valley. *Prunum maoense* and *P. latissimum*, which are considered to be an ancestor-descendant lineage (Nehm, 1998; see Systematic Paleontology, p. 38), both occur in brackish to shallow marine (0–40 m paleodepth) silts and sands. Based on their associations with grass-flat coral communities, seagrass-associated limpets, and the obligatory seagrass epibiont *Smaragdia*, it appears that *P. latissimum* and *P. maoense* were seagrass dwelling species, much like the Recent Caribbean marginellid *P. apicinum* (Menke, 1828). *Prunum latissimum* and *P. maoense* share many morphological similarities with *P. apicinum*, as noted by Maury (1917). *Prunum conforme* occurs in shallow to deep marine deposits (40–200 m paleodepth) associated with coral reefs. *Prunum christineladde* occurs only in very deep-water silts (>150m paleodepth). It is difficult to determine the paleoecological preferences of *P. aminum*, *P. gibsonsmithorum*, and *P. mauryense* because they occur in very few samples.

ONTOGENETIC VARIATION

Introduction

Marginellid gastropods are appropriate morphological systems for the study of ontogenetic variation because: (1) The shell preserves a nearly complete record of ontogeny (from intracapsular juvenile to reproducing adult); (2) The shell records the termination of growth associated with sexual maturity, thus distinguishing juvenile and adult shells; (3) Unlike many gastropod groups, marginellids do not remodel the shell interior (Nehm, 1998), thus preventing inaccuracies in x-radiographic studies of ontogenetic change within and among species. These attributes make the marginellid shell an excellent system for morphological and developmental research.

The description and study of ontogenetic variability is a fundamental component of systematic and evolu-

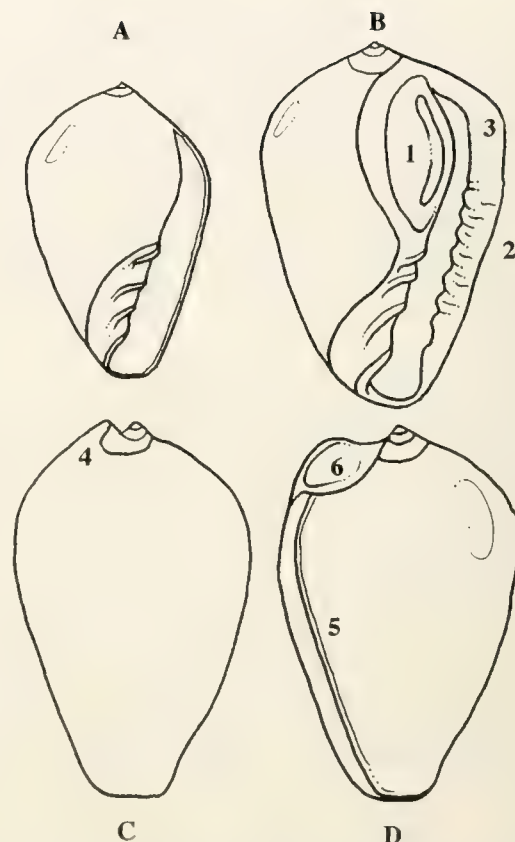
tionary research (Raup and Stanley, 1978, p. 55), yet it is absent from many contemporary paleontological studies. An understanding of ontogenetic variability is necessary for recognizing members of the same species at different ages and comparing morphological differences among individuals of similar ages. A comprehensive understanding of *Prunum* ontogeny at the species level is particularly important because: (1) Ontogenetic variation is important for species discrimination. Species-diagnostic characters, such as callus morphology, shape of the outer lip, presence of an external varix, and the presence and morphology of denticulations, are variable through ontogeny; (2) Juvenile stratigraphic and geographic distributions are not completely concordant with adult distributions, so assigning juveniles to species is necessary for accurately determining the temporal and geographic ranges of species; (3) Evolutionary change within populations, species, and clades is often generated by alterations in the timing of development (Williamson, 1987; McKinney and McNamara, 1991).

Separation of marginellid specimens into juvenile and adult classes is possible because living and fossil species, including *Prunum*, develop unique morphological features at adulthood, when growth in body size and shape ceases. In gastropods, determinate growth is recognized by the development of a lip varix, internal lip thickening, an ascending suture, and apertural callusing patterns (Vermeij and Signor, 1992). *Prunum* develops six morphological features at adulthood (Text-fig. 8): (1) An aperture margin callus; (2) Lip denticulations and/or crenulations; (3) Inner lip thickening; (4) A terminal inflection of the body whorl; (5) an external varix; and (6) A posterior lip callus. Importantly, size and shape are not characters used to identify adults and juveniles, thus it is possible to independently study size and shape changes through ontogeny in living and fossil species (see below).

Prunum coniforme, *P. christineladidae*, *P. maoense*, and *P. latissimum* are used to: (1) document morphological character variability and size/shape changes within species through ontogeny, (2) compare basic patterns of ontogenetic variation among species, and (3) establish a base for future work on heterochronic (temporal changes in developmental evolution) and heterotopic (spatial changes in developmental evolution) studies using Dominican *Prunum*.

Methods

Growth series are used to document morphological changes through ontogeny that are not visible using x-radiographs (e.g., the development of the body whorl callus). The construction of growth series involves illustrating and measuring a single "population" of each



Text-figure 8.—Morphological features that mark the termination of growth and permit the separation juvenile (e.g., A) and adult (e.g., B–D) *Prunum* shells: (1) An aperture margin callus; (2) Lip denticulations and/or crenulations; (3) Inner lip thickening; (4) A terminal inflection of the body whorl; (5) an external varix; and (6) a posterior lip callus.

species in different growth stages. A population refers to an assemblage of individuals of the same species from one stratigraphic horizon at one locality. Because of the similarity of the early ontogenetic stages of different *Prunum* species, populations of each species are sampled from a portion of their stratigraphic range that does not overlap with other *Prunum* species. This procedure minimizes potential mixing of juvenile shells from different species. Measurements were taken of maximum shell height and maximum shell width for juvenile and adult specimens.

X-radiographs of adult specimens lacking sediment inside the shell are used to document morphological changes in size and shape between each shell whorl. Shell whorl comparisons within populations and among species are convenient because *Prunum coniforme*, *P. christineladidae*, *P. maoense*, and *P. latissimum* each have four shell whorls. Measurements were taken of maximum shell height and maximum shell width for each shell whorl on the x-radiographs.

Results

1. Growth Series

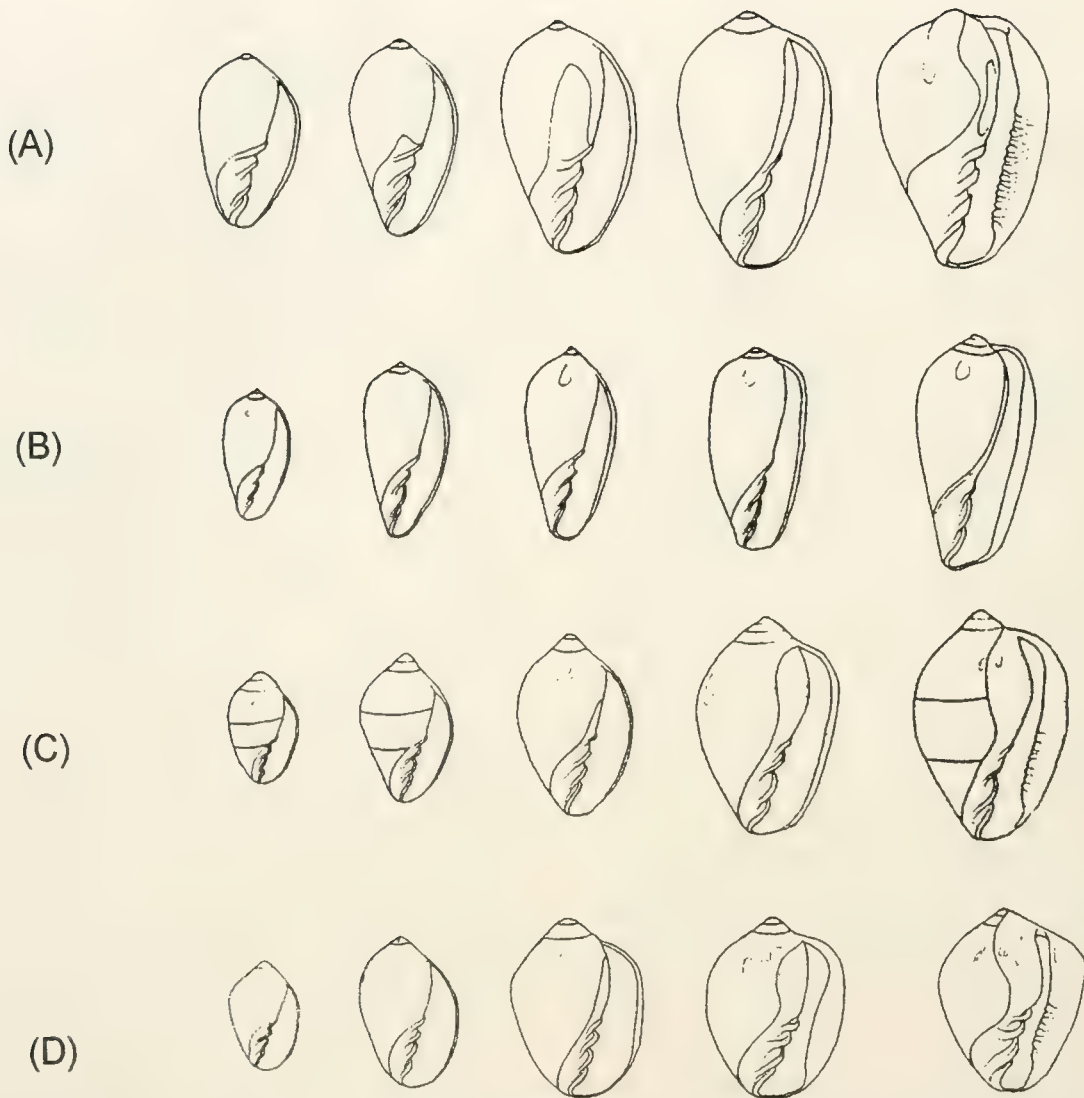
Prunum conforme (Text-fig. 9A).—The juvenile shell of *P. conforme* is strongly shouldered, the spire is nearly involute, and the outer lip is very thin and delicate. Through ontogeny, shells develop weak shouldering, short spires, and thick lips. Four thin and sharp columellar plications occur in the youngest (smallest, thinnest, and least-whorled) shells and thicken through ontogeny. There is no ontogenetic variation in the number of columellar plications. The callus covers the columellar plication area in the youngest shells studied. The most posterior border of the callus extends slightly above the edge of the most posterior plication in these shells. Through ontogeny, the area of the shell covered by callus expands substantially. Somewhat different patterns of callus expansion from the area of the columellar folds occur in different *Prunum* species. In *P. conforme* a large callus lobe extends from the area of the columellar folds and spreads in a posterior direction. This callus lobe eventually forms a long band along the aperture margin of the body whorl. Subsequently, this callus band thickens but does not expand in area. Callus processes (raised and distinct callus projections) are then deposited in specific and consistent locations on the shell. The most prominent process in *P. conforme* occurs on the posterior canal near the spire. A crescent shaped callus ridge is also deposited near the medial indentation of the aperture margin callus. The formation of the external varix and thickening of the inner lip coincide with deposition of the posterior callus process and ridge. Expansion of the inner lip and thickening of the apertural callus reduce the aperture area and change its shape. Lip denticulations and crenulations develop after the inner lip thickens.

Prunum christineladdae (Text-fig. 9B).—Juvenile shells of *P. christineladdae* are similar to those of *P. conforme*, but they are more strongly shouldered, more cylindrical in shape, and lack extensive callusing. As in the other Dominican species, juvenile shells have a very thin and delicate outer lip. Four sharp and thin columellar plications occur in the youngest (smallest, thinnest, and least-whorled) shells sampled and there is no variability in the number of columellar plications through ontogeny. Columellar plications thicken through ontogeny. Callusing is present in the area of the columellar plications in the youngest shells studied. The callus does not extend above the most posterior plication in juvenile shells. A callus band similar to the late juvenile stages of *P. conforme* occurs in adults of *P. christineladdae*. At adulthood however no callus ridges or processes develop in *P. christinelad-*

dae. In adults the aperture area decreases because of an expansion of the inner lip and apertural callus. Aperture area does not decrease as much as in the other three Dominican species studied. Lip denticulations are absent but mild crenulations form after the inner outer lip thickens.

Prunum maoense (Text-fig. 9C).—The juvenile shell of *P. maoense* is proportionally narrower than the adult shell, and the outer lip is very thin, delicate, and jagged. A small callus deposit surrounds the columellar plications on the anterior margin of the shell in the youngest (smallest, thinnest, and least-whorled) shells sampled. Four very thin and sharp plications occur in these shells and thicken through ontogeny. The number of plications does not vary through ontogeny. Two color bands are visible on the body whorl in the earliest stages of ontogeny in some specimens. Through ontogeny the callus extends from the plication area and expands to the aperture margin. This callus deposit thickens through ontogeny but does not develop any clearly defined processes or ridges. Expansion of the inner lip and apertural callus result in a reduction in the aperture area and a change in aperture shape. A medial indentation in the outer lip develops in the early stages of lip thickening in some specimens. Denticulations form in the middle of the inner lip after the inner lip thickens.

Prunum latissimum (Text-fig. 9D).—The juvenile shells of *P. latissimum* are strongly shouldered whereas adult shells are more weakly shouldered. The spire is nearly involute in juveniles but prominent in adults. The outer lip is very thin and delicate in juveniles and thick and strong in adults. Four thin and sharp plications occur in juveniles and become thick and blunt in adults. As in the other *Prunum* species, there is no variability in the number of columellar plications through ontogeny. Callus covers the columellar plication area of the anterior shell in the youngest shells studied. In juveniles, the most posterior border of the callus extends slightly above the edge of the most posterior plication. Through ontogeny, the area of the shell covered by callus expands substantially. Callus processes are subsequently deposited in specific and consistent locations on the shell. The most prominent process occurs near the posterior aperture margin. This callus process is much thicker than the body whorl and expands into the aperture. In some individuals, the callus covering the posterior aperture and lip forms a process nearly as prominent as the spire. The development of the external varix and thickening of the inner lip coincide with deposition of the posterior callus process. Expansion of the inner lip and thickening of the callus process greatly reduce the area and shape of the



Text-figure 9.—Growth series for (A) *P. conforme*, (B) *P. christineladdae*, (C) *P. maoense*, and (D) *P. latissimum*. Growth series are used to document morphological changes through ontogeny that are not visible using x-radiographs (such as callus development).

aperture. *P. latissimum* has the most extensive callusing of all the Dominican marginellid species.

In summary, Dominican *Prunum* species share several patterns of ontogenetic change. In all four species, shouldering decreases through ontogeny, spire height increases through ontogeny, and aperture area decreases through ontogeny. All species have four columellar plications throughout ontogeny. Additionally, they all share a plication callus in early ontogeny and an aperture margin callus in late ontogeny. Lastly, inner lip thickening occurs before the formation of the external varix in all four species. Through ontogeny, Dominican *Prunum* vary in the magnitude of aperture margin callus, the pattern of callus expansion from the area of the columellar plications, the amount of inner lip

thickening, and the number and size of callus processes. These four features are important because they influence the overall shape and area of the aperture.

In general, the early ontogenetic stages of Dominican *Prunum* (whorls one and two) share the greatest number of morphological features, whereas the late ontogenetic stages (whorls three and four) contain the most differences. Nevertheless, adult *P. christineladdae* are very similar to late-stage juveniles of *P. conforme*, and adult *P. maoense* are very similar to late-stage juveniles of *P. latissimum*. These patterns of ontogenetic change are consistent with pedomorphosis in both ancestor-descendent pairs (*P. conforme*-*P. christineladdae*, and *P. latissimum*-*P. maoense*). These patterns are corroborated by quantitative comparisons

of size and shape change through ontogeny (see below).

II. Size and Shape Change Through Ontogeny

Measurements of body size and shape change through ontogeny are plotted for populations of *Prunum coniforme*, *P. christineladidae*, *P. maoense*, *P. latissimum* and *P. dasum* in Text-figure 10. The morphological features used to differentiate juvenile and adult shells are illustrated in Text-figure 8. Text-figure 10A summarizes mean values for height/width for juveniles and adults of all five species. An arrow indicates increasing age.

Overall, all five species exhibit similar shape changes through ontogeny: juvenile shells are relatively narrower (have a higher height/width ratio) than adults. In addition, two other patterns are noteworthy. First, the juvenile shell shapes of *Prunum dasum*, *P. maoense*, and *P. latissimum* are not significantly different among species, but adult shapes are significantly different among species. That is, morphological divergence occurs in late ontogeny in this group of species. Second, adult specimens of *P. christineladidae* have shell shapes that are similar to juvenile specimens of *P. coniforme*. Text-figure 10 B–F also demonstrates that in all five *Prunum* species adult shell size is significantly different from juvenile shell size.

Text-figure 11A–F illustrates quantitative changes in mean shell height, width, and height/width between each shell whorl for *Prunum maoense* and *P. latissimum* (Text-figure 11 A–C), and *P. coniforme* and *P. christineladidae* (Text-figure 11 D–F). Whorls one to three are juvenile growth stages, whereas whorl four is the adult stage. In all species comparisons, height and width divergence increases with each consecutive whorl; the first whorls are not significantly different from one another. Increases in width between shell whorls are greater than increases in height between whorls, indicating that shells become proportionally wider with age. Patterns of shell shape change are very similar in *P. maoense* and *P. latissimum*, but *P. maoense* is always narrower than *P. latissimum*. Change in shell shape is greatest between the third and fourth whorl in *P. maoense* and *P. latissimum*. Similar patterns of shape change through ontogeny also occur in *P. coniforme* and *P. christineladidae*. In summary, all four species exhibit similar patterns of ontogenetic change even though the magnitudes of size and shape differ at each whorl. Morphological divergence among species is greatest between the third and fourth whorls.

Conclusions

The morphological and morphometric differences between juvenile and adult *Prunum* shells highlight

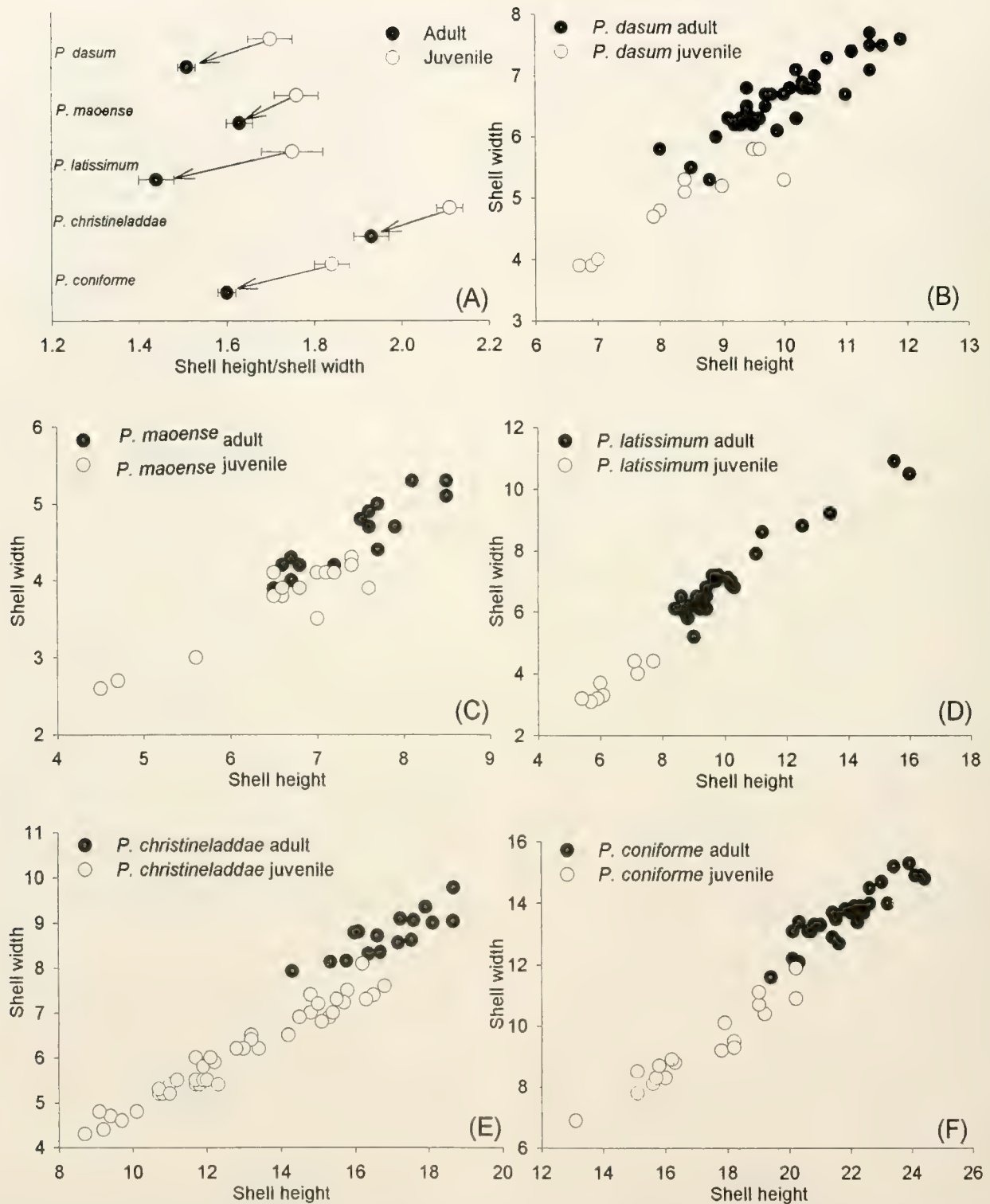
several important but often ignored points: (1) Malacological studies must include descriptions and illustrations of ontogenetic variation within species, for it is a fundamental aspect of systematic and evolutionary research; (2) Systematic or evolutionary comparisons of morphological differences between species must be made relative to similar ontogenetic ages or whorl numbers. Morphological comparisons of specimens of different ages or whorl numbers may reflect ontogenetic rather than evolutionary differences; (3) The large amount of ontogenetic variability present within species makes studies of spatiotemporal morphological variation difficult to interpret unless equivalent ontogenetic stages are compared; (4) Callus morphology is an underutilized source of phylogenetic information for *Prunum* gastropods. Callus characters are morphologically conservative and species-specific; (5) Ontogenetic patterns of callus development have great potential as characters in studies of the evolution of development (heterotopy and heterochrony; e.g., Nehm, 1998).

SPATIOTEMPORAL MORPHOLOGIC VARIATION

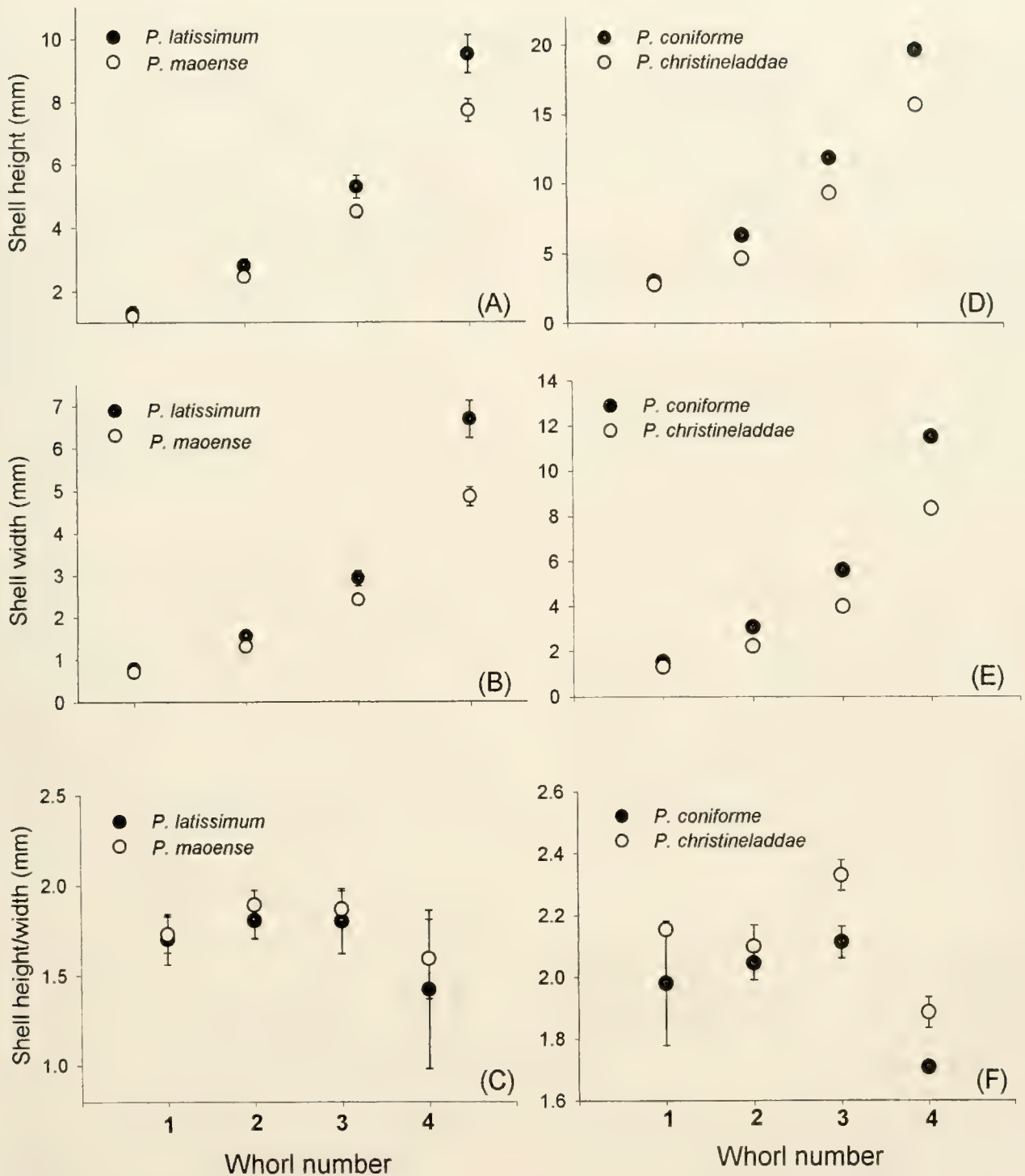
Introduction

The extensive geographic and temporal sampling of Dominican marginellid fossils, coupled with detailed paleoenvironmental and paleoecological data (see Paleoecology, p. 13), provide an opportunity to examine temporal and geographic patterns of morphological variation and their relationships to paleoenvironmental and paleoecological parameters. Shell size and shape variation in fossil *Prunum* species are also compared to size and shape variation in three living *Prunum* species from different habitats. Three specific questions are addressed: (1) Do Dominican *Prunum* species exhibit significant morphological changes in size and shape as paleoenvironmental and paleoecological conditions change *within* each river section? (2) Do Dominican species show significant morphological differences in size and shape *among* the river sections (e.g., geographic variation)? and (3) Do Dominican species exhibit comparable magnitudes of morphological variation in size and shape as living *Prunum* species?

Morphometric analyses are performed on samples of *Prunum maoense*, *P. latissimum*, *P. coniforme* and *P. christineladidae*, the most abundant and continuously occurring Dominican species, as well as the extant marginellids *P. apicinum* (Menke, 1828), *P. guttatum* (Dillwyn, 1817), and *P. prunum* (Gmelin, 1791). *Prunum apicinum* is an intertidal and shallow marine species that occurs throughout Florida and the West Indies. It occurs most abundantly in *Thalassia* beds



Text-figure 10.—(A). Mean values for height/width for juveniles and adults of five *Prunum* species. An arrow indicates increasing age. Error bars represent two standard errors about each mean. (B–F) Measurements of size (shell height) and shape (shell height/width) through ontogeny for populations of (B) *P. dasum*; (C) *P. maoense*; (D) *P. latissimum*; (E) *P. christineladdae*; and (F) *P. conforme*. Text-figure 8 illustrates the morphological features used to differentiate juvenile and adult shells; shell size and shape were not used to distinguish juveniles and adults.



Text-figure 11.—Quantitative changes in shell height, width, and height/width between each shell whorl for *P. maoense* and *P. latissimum* (A–C), and *P. conforme*, and *P. christineladdae* (D–F). Whorls one to three are juvenile growth stages, whereas whorl four is the adult stage.

and organic rich mud. *Prunum guttatum* is a shallow to deep marine species that occurs in Florida and the West Indies. This white and spotted *Prunum* inhabits coral reefs, coral rubble, and carbonate sand. *Prunum*

prunum, a southern Caribbean marginellid common in Venezuela and Colombia, occurs in shallow to deep marine environments in siliciclastic sediment and organic-rich mud.

Methods

Adult specimens of all seven species were separated from juvenile specimens using the six morphological features illustrated in Text-figure 8. All non-fragmented adult shells from each stratigraphic or geographic sample were mounted on cardboard trays in apertural view with the columellar axis oriented horizontally to the surface. Shell size and shape were measured using Scion Image[®] software. Maximum shell height was used as a proxy for shell size, and maximum height/maximum width was used as a proxy for overall shell shape (globosity). Considerable morphometric work has shown that (1) these simple measurements yield results that are comparable with multivariate analyses, and (2) these measurements describe the simple form of the marginellid shell accurately. (Traditional and geometric morphometric multivariate analyses are more appropriate for other systematic and evolutionary questions [Nehm, 1998]).

Means, standard errors, and coefficients of variation (CV) were calculated for shell size (shell height) and shell shape (shell height/shell width) for all measured samples of living and fossil species. Samples were tested for significant differences using an Analysis of Variance (ANOVA) in SYSTAT 7.0 (SPSS, Inc). In cases of significant differences among samples detected by ANOVA, Tukey's *post-hoc* HSD method of pairwise comparisons was used to identify the location of significant between-sample differences (Wilkinson, 1996). The HSD method is the most appropriate (and sensitive) test to use to test for between-sample differences when large numbers of samples are compared (Wilkinson, 1996, p. 133).

Results

Although some sample differences may appear significant on plots because of non-overlapping 95% confidence intervals (e.g., Text-fig. 12), after adjustment for multiple comparisons using the Tukey HSD method, only some of these differences remained statistically significant (e.g., Text-fig. 13).

1). *Prunum maoense* (Text-fig. 12A–D; Text-fig. 13).—Plots of shell size and shape through the Río Cana and Río Gurabo sections indicate that no net morphological change occurs in *P. maoense* (Text-fig.

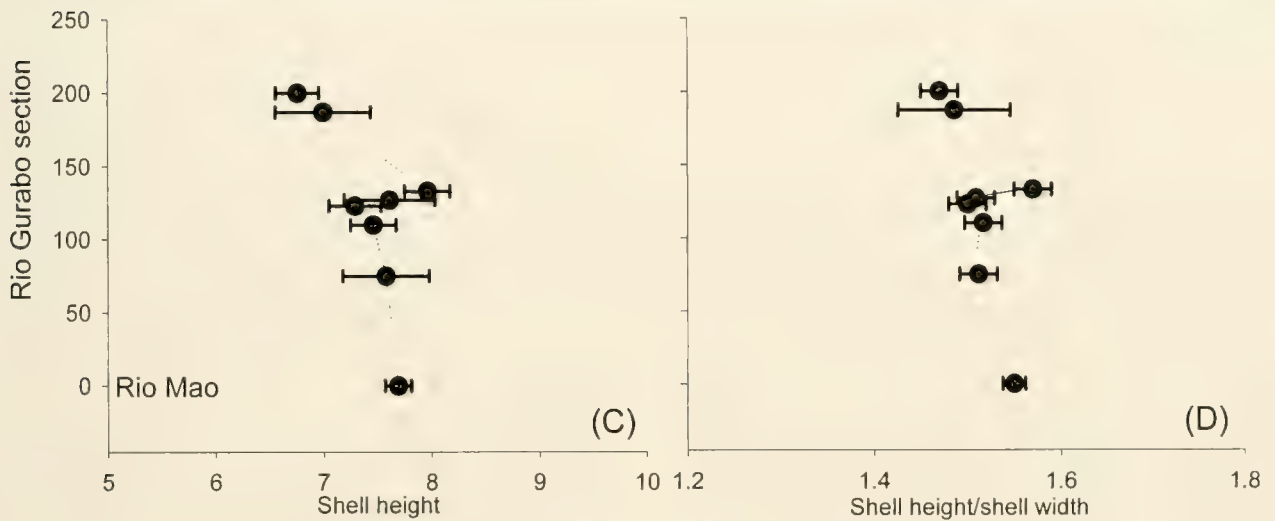
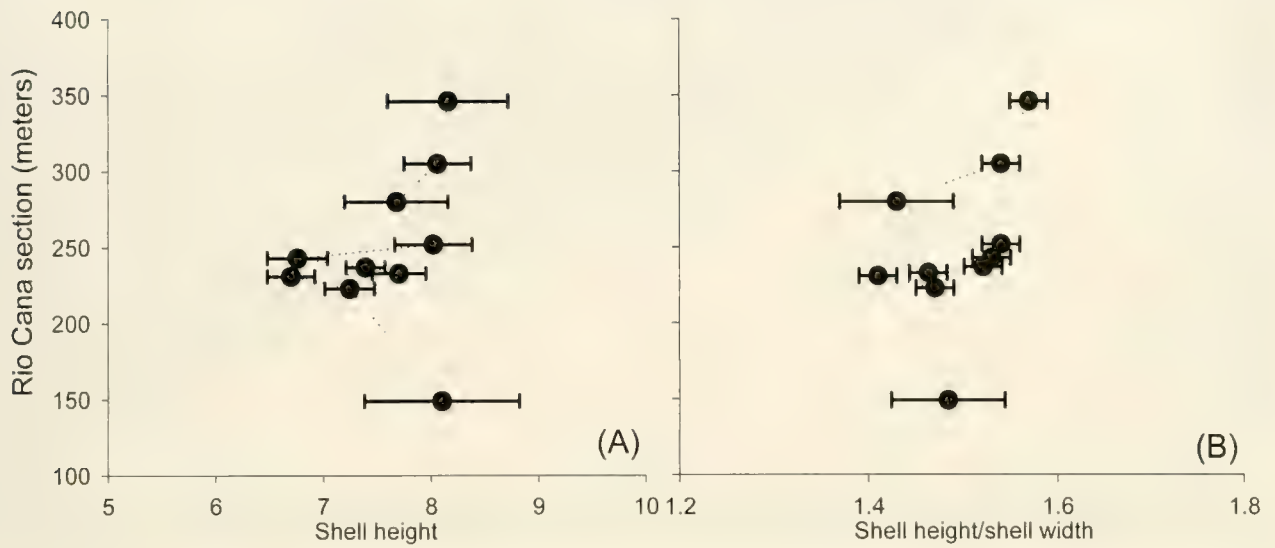
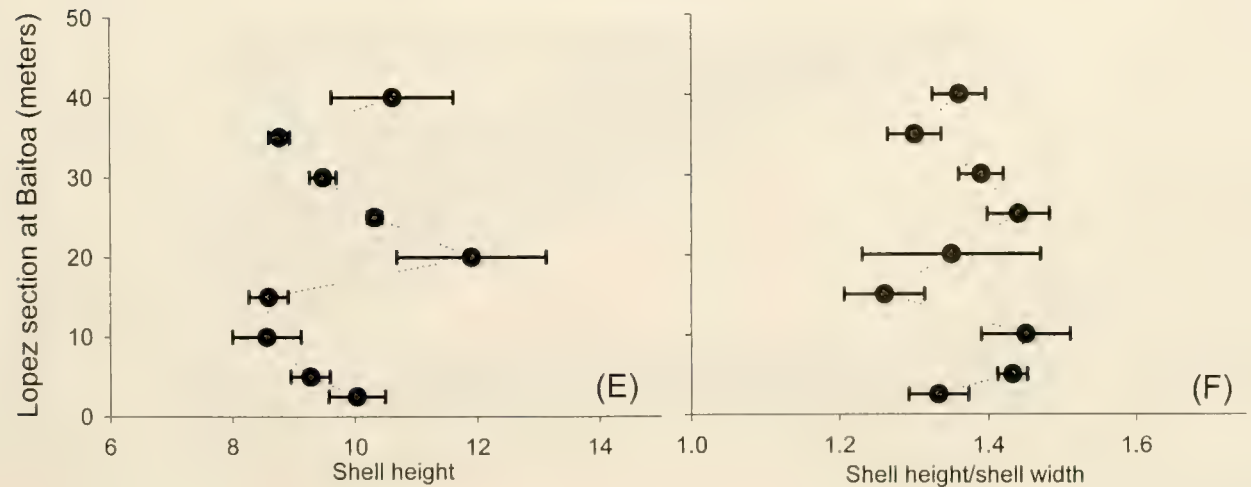
12, A–D). ANOVAs of shell size and shape, however, were significant ($p < .0001$). *Post-hoc* tests revealed the locations of significant sample differences within and among the stratigraphic sections (Text-fig. 13). Although the distribution of significant differences does not follow any pattern, some significant sample differences are noteworthy. In the Río Cana section, specimens from near 230 m in the section are significantly smaller and proportionally more cylindrical (less globose) than many other samples, but the morphological changes during this interval were transitory (Text-fig. 12A–B; Text-fig. 13). Samples from above 180 m in the section are smaller than many other samples (Text-fig. 12C–D; Text-fig. 13). Overall, no consistent morphological differences occur among samples from the Río Cana, Río Gurabo, and Río Mao sections. In addition, the distribution of significant sample differences appear random within the Río Cana or Río Gurabo sections, indicating a lack of significant directional anagenetic change.

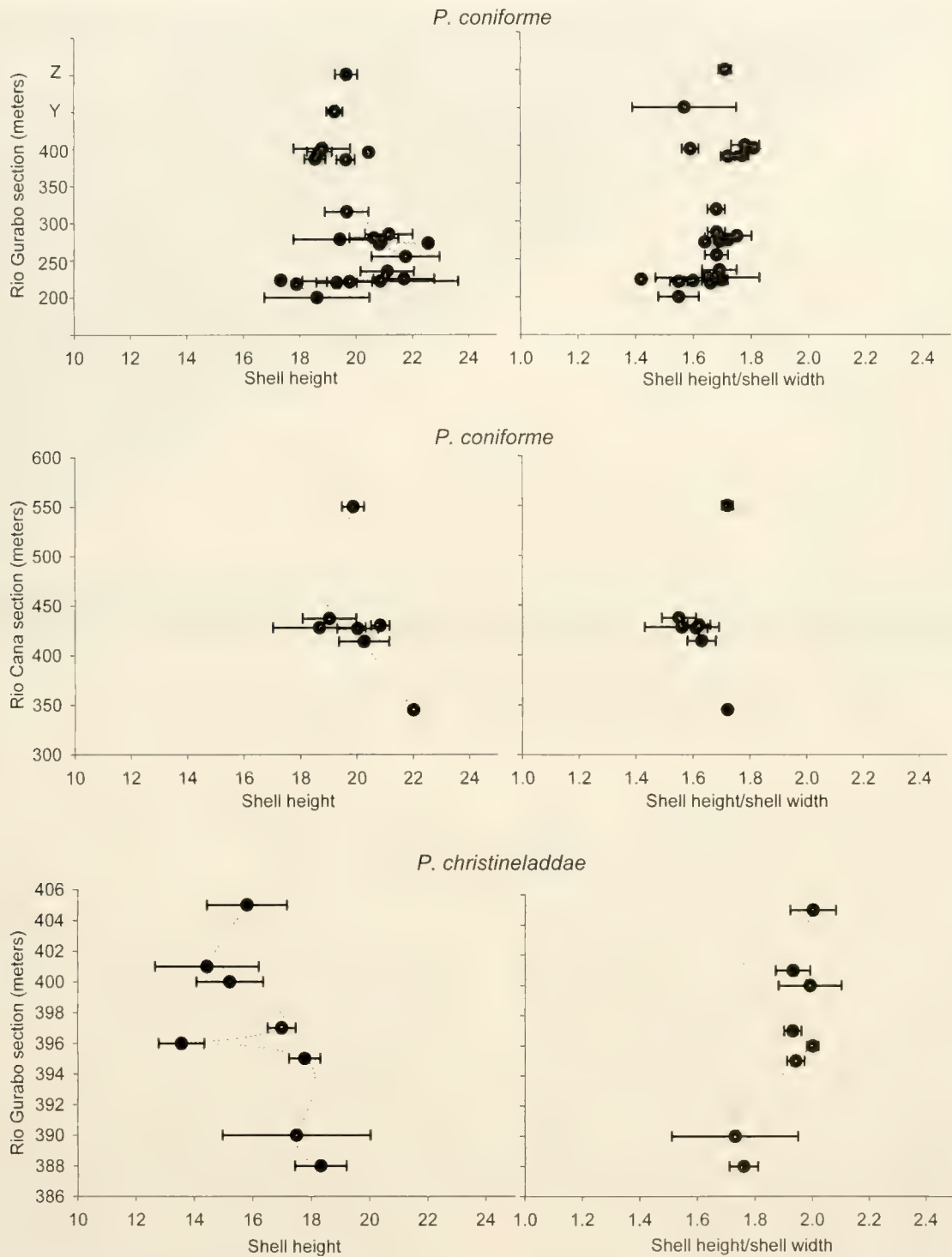
2). *Prunum latissimum* (Text-fig. 12E–F; Text-fig. 14).—Plots of shell size and shape through the López section at Baítoa indicate that, despite pronounced morphological oscillations in size and shape through time, no net or long-term directional morphological change occurs in *P. latissimum* (Text-fig. 12, E–F). ANOVAs of shell size and shape were significant ($p < .0001$), and *post-hoc* tests revealed the location of significant sample differences (Text-fig. 14). Specimens from samples near 20 m and 40 m in the section are significantly larger than specimens from most other samples, whereas specimens collected from samples near 15 m and 35 m are significantly smaller than specimens from most other samples. A trend of size decrease occurs from 20 m to 35 m in the section. (Text-fig. 12E–F; Text-fig. 14).

Several populations of *Prunum eleutherium dasum* (Gardner, 1928) from the Lower to Middle Miocene Chipola Formation of Florida are very similar to *P. latissimum* (see Systematic Paleontology, p. 37) and were therefore included in morphological comparisons of Dominican populations. In general, the Florida samples show only a few significant differences in size and shape from the Dominican samples.

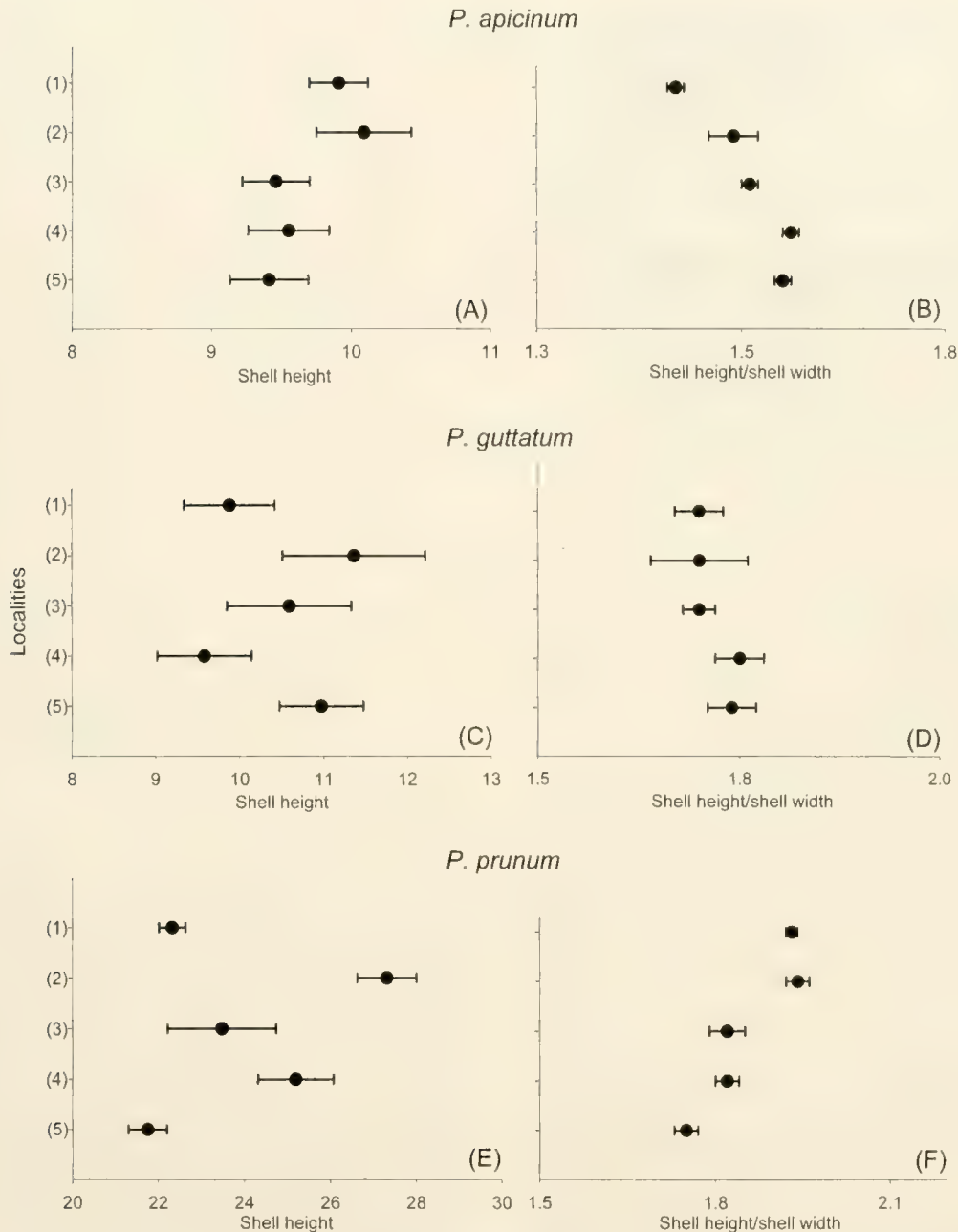
As with *Prunum maoense* in the Río Cana, Río Gur-

Text-figure 12.—Shell size and shape change through time in *P. maoense* in the Río Cana section (A–B) and Río Gurabo section (C–D). Shell size and shape change through time in *P. latissimum* in the Río Yaque del Norte section at López (E–F). Filled circles represent mean values for each sample. Two standard errors about the mean are also illustrated. *N. B.* While some sample differences may appear significant on plots because of non-overlapping 95% confidence intervals, after adjustment for multiple comparisons using the Tukey HSD method, only a fraction of these differences remained statistically significant (e.g., Text-fig. 13 and 14).

P. maoense*P. latissimum*



Text-figure 15.—Shell size and shape change through time in *P. conforme* in the Río Gurabo section (A–B) and the Río Cana section (C–D). Shell size and shape change through time in and *P. christineladdae* in the Río Gurabo section (E–F). Filled circles represent mean values for each sample. Two standard errors about the mean are also illustrated. *N. B.* While some sample differences may appear significant on plots because of non-overlapping 95% confidence intervals, after adjustment for multiple comparisons using the Tukey HSD method, only a fraction of these differences remained statistically significant (*e.g.*, Text-fig. 16).

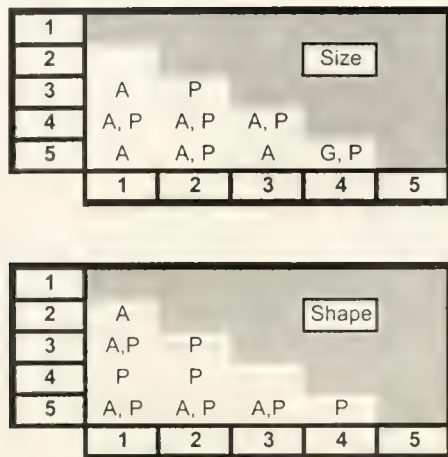


Text-figure 17.—Shell size and shape differences in living populations of *P. apicinum* (A–B), *P. guttatum* (C–D), and *P. prunum* (E–F). Filled circles represent mean values for each sample. Two standard errors about the mean are also illustrated. *N. B.* While some sample differences may appear significant on plots because of non-overlapping 95% confidence intervals, after adjustment for multiple comparisons using the Tukey HSD method only a fraction of these differences remained statistically significant (e.g., Text-fig. 18).

tions (from shallow to deep marine paleoenvironments) shell size and globosity do not change accordingly. Within-section morphological evolution in *P. maoense* and *P. latissimum* is characterized by: (a) the absence of *net* morphological change; (b) randomly-distributed between-sample differences; and (c) the absence of long-term morphological trends. A wide array

of processes could account for these patterns, including stabilizing selection, genetic drift, constraint, or a combination thereof (Nehm, 1998).

In *P. coniforme*, shell size and globosity to not change in response to environmental change for most of its stratigraphic range. However, in the middle Gurabo Formation of the Río Gurabo, directional morpho-



A = *P. apicinum* $p < 0.01$

G = *P. guttatum* $p < 0.01$

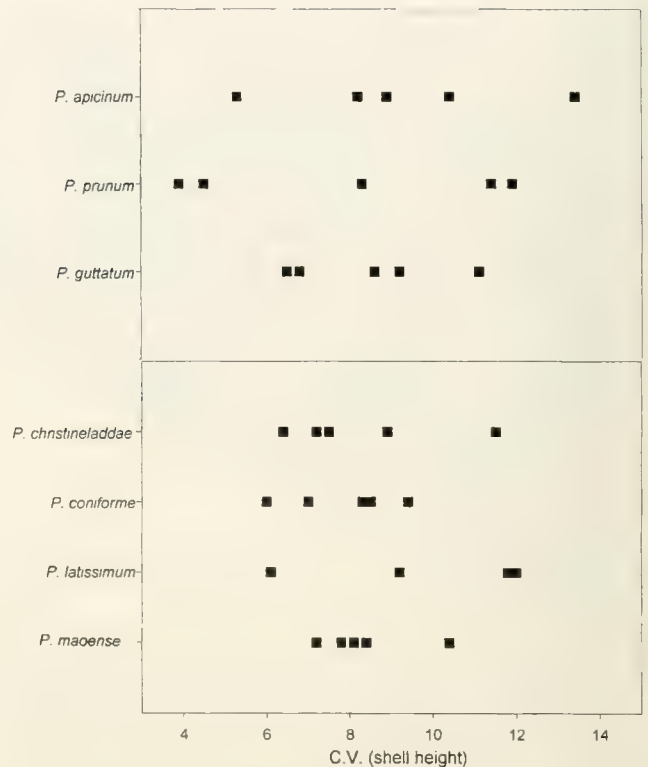
P = *P. prunum* $p < 0.01$

Text-figure 18.—ANOVAs of shell size and shape for living populations of *P. apicinum*, *P. guttatum*, and *P. prunum*. Significant results for sample pairwise comparisons ($p < .01$) for shell size (height) are indicated by the first letter of each species, as are significant results for shell shape (height/width). "A" = *P. apicinum*; "G" = *P. guttatum*; "P" = *P. prunum*.

logical changes do occur in *P. conforme* (Nehm and Geary, 1994); few other samples demonstrate significant morphological differences within the Río Cana or Río Gurabo sections. Directional morphological change in *P. conforme* may have been produced by genetic drift or directional selection (Nehm and Geary, 1994).

(2) *Geographic variation.* Dominican *Prunum* species do not show significant morphological differences in size and shape *between* river sections. Although some significant differences occur in shell size and shape between samples from different river sections, *P. conforme* does not exhibit any clear or consistent pattern of geographic variation. In addition, samples from the Upper Pliocene Bowden Formation of Jamaica (2–3.5 Ma) are not significantly different from samples from the Dominican Republic (Nehm and Geary, 1994). *Prunum maoense* demonstrates similar morphological patterns to those of *P. conforme*: a number of significant morphological differences occur between samples from different river sections, but no clear or consistent pattern of geographic variation is observed.

(3) *Intraspecific variation.* Dominican *Prunum* species display comparable magnitudes of adult intraspecific morphological size variation as living *Prunum* species. Coefficients of Variation (CV) indicate that adult shell size variability is much greater than shape

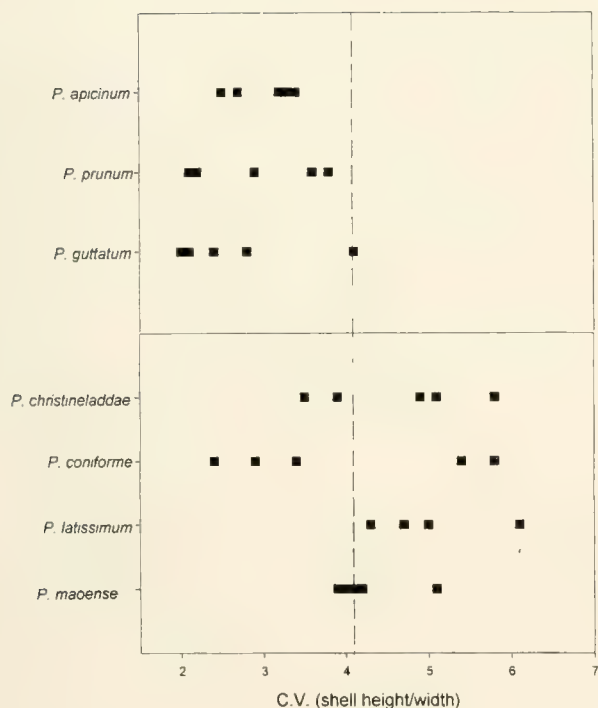


Text-figure 19.—Coefficients of variation for shell height for living and fossil samples of *Prunum*.

variability in all living and fossil species (Text-fig. 19 and 20). Comparisons of adult shell size variability within living and fossil species indicate that Dominican fossil species exhibit comparable magnitudes of variability as living species (Text-fig. 19). In contrast, comparisons of adult shell globbosity within living and fossil species indicate that globbosity is much greater in all four Dominican fossil species than in the three living species (Text-fig. 20). More research is necessary in order to determine the cause(s) of this pattern as well as its systematic and evolutionary implications.

BIOGEOGRAPHY

Over half of Dominican *Prunum* species are endemic (*P. christineladdeae*, *P. mauryense*, *P. gibsonsmithorum*, *P. aminum* and? *P. domingoense*). Several lines of evidence suggest this endemism is not a result of preservational bias in the fossil record: (1) contemporaneous deposits in Haiti, Jamaica, and Central America lack some Dominican species; (2) the invertebrate fauna of the Neogene sections of the Cibao Valley contains many endemic species, suggesting some degree of isolation from surrounding regions (Woodring, 1928, 1970, 1974; Vokes, 1979; Petuch, 1981, 1982; Jung and Petit, 1990); (3) all living mar-



Text-figure 20.—Coefficients of variation for shell height/width for living and fossil samples of *Prunum*.

marginellid gastropods studied to date (including *Prunum*) are direct developers; pelagic larvae have never been observed in the family (Coovert, 1987). Fossil marginellids, like extant direct developers, have paucispiral protoconchs. Because they develop directly and are not planktonic, living marginellid species are often confined to single geographic provinces and have restricted geographic ranges (Coovert, 1987).

Those Dominican species that are not endemic to the Cibao Valley occur in Haiti, Jamaica, and Florida. *Prunum maoense* and *P. conforme* from the Cercado, Gurabo and Mao Formations of the Dominican Republic also occur in the Upper Miocene Thomonde Formation of Haiti and the Upper Pliocene (2–3.5 Ma) Bowden beds of Jamaica. *Prunum latissimum* from the Baitoa Formation of the Dominican Republic may also occur in the Lower to Middle Miocene Chipola Formation (15–18 Ma) of Florida. These distributions indicate that Dominican species appear to be confined to the Caloosahatchian Faunal Province (Woodring, 1974; Petuch, 1982).

SYSTEMATIC PALEONTOLOGY

Introduction

The systematic assumption of this study is that the magnitude of morphological variation between living marginellid species provides an accurate benchmark

for the delineation of fossil marginellid species (Nehm and Geary, 1994; Nehm, 1998; *Spatiotemporal Morphologic Variation*, p. 19). Both continuous and discrete shell characters are necessary for the identification of living marginellid species (Nehm, 1998). Previous research on Dominican *Prunum* focused on the use of continuous morphological characters in species delineation (Nehm and Geary, 1994; Nehm, 1998). This study expands our understanding of the systematics of Dominican fossil marginellids by: (1) generating a suite of discrete characters and character states and noting their distribution among species (Table 1); (2) diagnosing species using autapomorphic character states (that is, character states that are not known to occur in other living or fossil species); and (3) studying and comparing the magnitude of morphological variation within Dominican species to the variation within three living species from different environments and geographies (see *Spatiotemporal Morphologic Variation*, p. 19). These new approaches enhance our confidence that the fossil species delineated here approximate biological species.

No attempt is made to place Dominican *Prunum* species in subgeneric groupings or clades. Although *Volvarina* and *Prunum* species collectively form a well-supported monophyletic group in cladistic analyses of morphological and molecular data (Coovert and Coovert, 1995; Nehm and Simison, unpublished data) the monophyly of each genus is not well established and species-level relationships are poorly understood (Nehm, in press; Nehm and Simison, unpublished data). Therefore, species-level phylogenetic analyses of *Prunum* and *Volvarina* are necessary before more detailed classification schemes can be erected. The characters and character states presented here are a first step in achieving this goal.

Family MARGINELLIDAE Fleming, 1828

Diagnosis.—(Coovert and Coovert, 1995, p. 75). Shell minute to large, white or patterned. Protoconch paucispiral. Lip thickened, smooth or denticulate. External varix present or absent. Siphonal notch present or absent. Columellar folds continuous internally. Columella with 2–6 folds. Internal whorls not remodeled. Type 1 or 2 animal (Coovert and Coovert, 1995, p. 52). Operculum absent. Radula type 5, 6, 7, 8 or 9 (Coovert and Coovert, 1995, p. 56). Mantle cavity with monopectinate ctenidium and bipectinate osphradium. Proboscis pleurembolic, buccal pouch present, absent in aradulate species. Odontophore cartilages fused anteriorly or anteriorly and posteriorly. Valve of Leiblein present or absent, with or without bypass tube. Gland of Leiblein large and saccate emptying into posterior esophagus or bypassing through the nerve ring and

Table 1.—Characters and character states used for diagnoses and descriptions of Dominican *Prunum* species.

Morphological feature	Character state	Dominican species						
		<i>P. aminum</i>	<i>P. gibson-smithorum</i>	<i>P. conforme</i>	<i>P. christine-laddae</i>	<i>P. maoense latissimum</i>	<i>P. maoense maurvense</i>	<i>P. domingense</i>
Shell size	small (1–10mm) = 0 medium (10–20mm) = 1 large (20–30mm) = 2	2	2	1, 2	0, 1	0	0	2
Dorsal shell shape	obovate (height/width < 1.8) = 0 cylindrical (height/width > 1.8) = 1	1	0	0	1	0	1	0
Shell shape-lateral	weakly domed = 0 strongly domed = 1 triangular = 2 trapezoidal = 3	0	0	0	0	0	0	0
Shell thickness	thick (thickness/width > .1) = 0 thin (thickness/width < .1) = 1	1	1	1	0	1	1	1
Shouldering	strongly shouldered = 0 weakly shouldered = 1	1	0	0	0	1	1	2
Spire height	involute (0–5% of height) = 0 short (5–10% of height) = 1 tall (10–20% of height) = 2	0	0	0	0	0	0	0
Anterior sinus	present, strong = 0 present weak = 1 absent = 2	1	1	1	0	1	1	0
Aperture shape	semicircular = 0 narrow, conforms to body whorl = 1 dumbbell shaped = 2 curved = 0 flat and flanged = 1 no color present = 0 stripes = 1 spots = 2 four folds = 0 five folds = 1 > five folds = 2	0	0	0	0	0	0	0
Ventral surface morphology	<.5 of aperture = 0 >.5 aperture = 1 present = 0 absent = 1 present = 0 absent = 1 uniform = 0 nonuniform = 1 none = 0	0	0	0	0	0	0	0
Coloration	lip attachment callus present = 1 spire callus present = 2 peripheral callus ring present = 3	0	0	0	0	0	0	0
Columellar fold number		0	0	0	0	0	0	0
Columellar position in aperture		0	0	1	1	1	1	1
Anterior fold lip margin expansion		1	1	1	1	1	1	1
Posterior fold canal		1	1	1	1	1	1	1
Columellar fold spacing		0	0	0	0	1	1	0
Dorsal callus features		1	1, 2	1	0	1	1	1

Table 1.—Continued.

Morphological feature	Character state	Dominican species						
		<i>P. aminum</i>	<i>P. gibson-smithorum</i>	<i>P. conforme</i>	<i>P. christine-laddae</i>	<i>P. maoense latissimum</i>	<i>P. mauryense domingoense</i>	
Posterior sinus callus process	present = 0 absent = 1	1	1	0	1	1	1	1
Inner apertural callus ridge	present = 0 absent = 1	1	0	1	1	1	1	1
Callus filled fold interspaces	present = 0 absent = 1	1	0	1	1	1	1	1
Ventral spire callus	absent = 0 partial coverage = 1 total coverage = 2	1	2	1	0	1	0	1
Ventral callus area on body whorl	none = 0 columellar fold area only = 1 posterior aperture margin = 2 all of aperture margin = 3 total ventral surface = 4	3	3	3	1	2	3, 4	3
Denticulation coverage	absent = 0 anterior lip = 1 medial lip = 2 total lip = 3	3	2	2	0	2	2	2
Denticulations extend into aperture	present = 0 absent = 1	0	1	1	1	1	1	1
Lip shape in cross section	triangular = 0 straight = 1	0	0	0	1	0	0	1
Denticulation shape	absent = 0 irregular = 1 uniform = 2	1	1	1	0	1	1	0
Crenulations	present = 1 absent = 0	0	0	1	1	0	0	0
External varix	present = 1 absent = 0	1	1	1	1	1	1	1
Lip height in relation to spire	above = 0 below = 1	1	1	2	0, 2	1	1	1
Outer lip angulation	same height = 2 <75 degrees 75–90 degrees >90 degrees	1	1	1	1, 2	0	0	0

emptying into anterior end of proboscis. Paired salivary glands present. Single accessory salivary gland present or absent. Anal gland present.

Subfamily **MARGINELLINAE** Coan, 1965

Diagnosis.—(Coover and Coover, 1995, p. 80). Shell minute to very large, white or patterned. Lip thickened, smooth or denticulate. External varix present or absent. Siphononal notch present or absent. Columella with 2–6 plications. Type 2 animal (Coover and Coover, 1995, p. 52). Mantle smooth, pustulose or papillose. Radular Types 6, 8, 9 or no radula (Coover and Coover, 1995, p. 56). Odontophoral cartilages fused anteriorly or both anteriorly and posteriorly. Valve of Leiblein present or absent, if present with bypass tube. Esophageal caecum present or absent. Gland of Leiblein with long duct and terminal bulb. Paired salivary glands. Single accessory salivary gland present or absent.

Tribe **PRUNINI** Coover and Coover, 1995

Diagnosis.—(Coover and Coover, 1995, p. 89–90). Shell small to very large, white, uniformly colored, patterned, or banded; spire immersed, or low to tall; lip thickened, smooth to denticulate; external varix present or absent; siphonal notch usually absent; posterior notch absent; columella with 2–6 plications occupying half or less of aperture. Type 2 animal; siphon long to very long; mantle smooth, pustulose, rarely distinctly papillose, usually extending over shell surface. Type 6 radula or aradulate. Buccal pouch present, absent in aradulate species. Odontophoral cartilages fused anteriorly or both anteriorly and posteriorly; valve of Leiblein absent; esophageal caecum present; gland of Leiblein with long convoluted duct and terminal bulb, passing through nerve ring, emptying into anterior end of proboscis. Paired salivary glands, ascinous or tubular, contained within proboscis or free. Ducts either attached to walls of esophagus or free; single accessory salivary gland present or absent, ascinous or tubular.

Genus **PRUNUM** Hermannsen, 1852

Hermannsen, 1852, p. 113

Type species.—*Voluta prunum* Gmelin 1791, by monotype and tautotype. Recent, southern Caribbean (Venezuela, Colombia, and Trinidad).

Diagnosis.—Shell small to large, usually thick. Opaque white or uniformly colored, often patterned with dark narrow bands. Spire tall to nearly involute. Lip moderately to strongly thickened, smooth or denticulate. External varix present. Siphonal notch usually absent. Posterior notch absent. Shell with heavy ventral callusing. Columella with four plications occupy-

ing less than half of the aperture. Type 2 animal (Coover and Coover 1995, p.52); siphon long to very long. Mantle smooth, extending over external shell surface. Type 6 radula (Coover and Coover, 1995, p. 56).

Remarks.—*Prunum* is one of the most diverse marginellid genera. Based on data from Rosenberg (1993), Coover (personal communication, 1996), and the literature, there are from 52 to 80 species of *Prunum* and *Volvarina* in the Tropical Western Atlantic. In contrast, only 12 species of *Prunum* and *Volvarina* are known from the tropical eastern Pacific. The western Atlantic and eastern Pacific contain more than 90% of all living and fossil species of *Prunum* (see Lipe, 1991; Coover and Coover, 1995). The Neogene fossil record of western Atlantic and eastern Pacific *Prunum* is extremely rich in terms of individual specimens and species. About 50 species have been described from the Neogene of tropical America, most of which are now extinct. *Prunum* is rare in Paleogene deposits but common in Neogene deposits of tropical America. *Prunum* occurs in the Oligocene of Panama (Woodring, 1970) and the Oligocene of Florida (Portell, personal communication 1994). Records of fossil *Prunum* from outside of tropical America are questionable. Several *Prunum* species have been described from the Eocene of Pakistan and Egypt (Eames, 1923). These species have involute spires and five or more columellar plications. These features are diagnostic of the marginellid genus *Cryptospira* (Hinds, 1844).

Prunum aminum (Dall, 1896)

Plate 2, figures 5, 7

Marginella aminum Dall 1896, p. 309, pl. 29 fig. 15; Maury, 1917a, p. 236.

Original description.—"Shell elongated, heavy, somewhat attenuated in front, with about 4 whorls; surface smooth, polished, spire rather more pointed and distinct than in *M. limonense*, and with less enamel on it; aperture narrow, nearly straight, nearly as long as the shell; not widened behind; outer lip thick and heavy, profusely crenulated from end to end, on the outside with a very deep profoundly excavated sulcus, except above the shoulder, where there is a thick callous deposit; pillar lip with a wash of callus, anteriorly with 4 plaits, the posterior pair transverse, the anterior oblique, enlarging forward; canal wide, excavated. Lon. 25, lat. 13 mm. Potrero, Río Amina, Santo Domingo, in Oligocene beds, Bland. This species is shorter, broader, and heavier than *M. limonensis*, from which it is further distinguished by its strongly crenulated lip and the extremely deep sulcus behind the lip." (Dall, 1896, p. 309).

Description (Table 1).—Shell large (20–30 mm), obovate (height/width < 1.8), weakly domed in lateral view. Shell thick, weakly shouldered, with short spire (< 5–10% of height). Anterior sinus absent. Aperture narrow, generally conforming to shape of body whorl. Ventral surface of shell curved, lacking flanging. No color pattern visible. Four columellar folds present, occupying less than half of aperture. Anterior fold does not expand but forms uniform rim on anterior aperture. Posterior fold canal absent. Columellar folds generally uniformly spaced. Lip attachment callus present on dorsal surface of shell. Posterior sinus callus process and inner apertural callus ridge absent. Callus-filled fold interspaces absent. Ventral surface of spire partially covered with callus; aperture margin completely covered with thin callus. Large, irregular denticulations extending into aperture present on entire lip, including anterior lip margin. Lip triangular in cross section. Crenulations absent. External varix present. Lip attaches below spire and angled <60 degrees from columellar axis.

Type material.—Holotype, USNM 113773. Figured in Plate 2, figure 5.

Type locality.—Potrero, Río Amina, Dominican Republic (Guppy and Dall, 1896).

Material.—Measured and/or figured specimens: USNM 113773, NMB locality 16936, and TU 1363. Specimens are cataloged by locality and listed in the Occurrence section.

Measurements.—Holotype: Height 25 mm, width 13 mm.

Comparisons.—*Prunum aminum* (Menke, 1828) is one of three large *Prunum* species known to occur in the Dominican Republic Neogene. *Prunum gibson-smithorum* is larger, more cylindrical, and has callus covering the entire ventral surface of the shell in a long band that fills the columellar fold spaces. Unlike other Dominican *Prunum* species, the denticulations of *Prunum aminum* occur throughout the aperture. *Prunum coniforme* has a wider body whorl, a posterior sinus callus process, and a crescent shaped callus ridge in the middle of the aperture margin. A large inflection in the body whorl callus is also present in *P. coniforme* and absent in *P. aminum*. *P. aminum* is similar to *P. aurorum* (Dall, 1890) from the Chipola Formation of Florida, but *P. aurorum* has different callus patterns on the ventral surface, a more angled outer lip, and a much wider aperture than *P. aminum*.

Remarks.—Maury apparently did not collect this species, but reports it to be “collected by Bland at Potrero, Río Amina” (Maury, 1917b). Since then only six specimens of *P. aminum* have been collected in the Dominican Republic.

Occurrence.—This species was collected from the

following NMB and TU localities (see Stratigraphic Distribution, p. 9, and Saunders *et al.* [1986] for locality information): Río Yaque del Norte at López, Baitoa Formation: NMB locality 16936, TU 1363, TU 1364.

Stratigraphic distribution.—Lower to Middle Miocene Baitoa Formation, Dominican Republic.

Geographic distribution.—Dominican Republic.

***Prunum christineladdae* (Maury, 1917a)**

Plate 2, figures 4, 8.

Marginella christineladdae Maury, 1917a, p. 234, pl. 11, fig. 6.

Original description.—“Shell slender, elongate, four-whorled, smooth and polished, spire very low; aperture nearly as long as the shell, narrow; margin of outer lip thickened, smooth within; inner lip of adult shells with a thin callus extending to the tip of the spire, columella with four plications, the three anterior oblique, the posterior transverse, lying at the center of the inner lip. Length of largest shell 19, width 9 mm.” (Maury, 1917a, p. 234).

Description (Table 1).—Shell small to medium sized (5–20 mm), cylindrical in shape (height/width >1.8 mm) with very weakly domed shape in lateral view. Shell thin, strongly shouldered, with involute spire (0–5% of shell height). Anterior sinus absent. Aperture wide and semicircular. Inner lip does not conform to body whorl. Ventral surface of shell slightly rounded, lacking flanging or flattening. No visible color pattern. Four columellar folds present throughout ontogeny, occupying more than half of aperture. Anterior fold does not expand, but is uniform in width and forms weak rim at anterior aperture margin. Canal absent posterior to fourth columellar fold. Four columellar folds nearly uniformly spaced, with posterior-most fold nearly horizontal. In dorsal view, both spire callus and large lip attachment callus are absent. Small callus band parallel to lip and posterior sinus callus process absent, as is an inner apertural callus ridge along body whorl. Callus does not fill columellar fold interspaces. Ventral surface of spire not covered with callus. On ventral surface of body whorl, callus generally restricted to columellar folds area. Denticulations absent, lip nearly straight in cross section. Lip crenulations present on most of lip, and external varix present but often poorly developed. Lip attaches at same level as spire, but highest point on lip higher than spire. Lip is angled from body whorl at about 110 degrees from columellar axis.

Type material.—Holotype PRI 28682. Figured in Plate 2, figure 4.

Type locality.—Zone B, Río Gurabo at Los Quemados, Dominican Republic (Maury, 1917a).

Material.—Measured and/or figured specimens: PRI

28682, NMB 15818. Other specimens are cataloged by locality and listed in the Occurrence section.

Comparisons.—*Prunum christinelladae* shares many morphological features with the marginellid genus *Volvarina* (Hinds, 1844). In general, *Prunum* shells are large, thick, obovate, heavily callused and denticulate, with thick and externally varixed lips. *Volvarina* shells are usually small, thin, cylindrical and often lack many features present in *Prunum*, including ventral callusing, denticulations, lip thickening, and the external varix. It is interesting to note that *P. christinelladae* generally develops a greater resemblance to typical *Volvarina* species as paleodepths increase in the Río Gurabo section. No other *Prunum* species (extant or extinct) have been observed to develop the morphological features of *Volvarina* in deep water environments.

Occurrence.—This species was collected from the following NMB and TU localities (see Stratigraphic Distribution, p. 9, and Saunders *et al.* [1986] for locality information):

Río Gurabo: Gurabo Formation. NMB localities 15803, 15805, 15806, 15807, 15809, 15810, 15811, 15812, 15813, 15816, 15817, 15818, 15820, 15837, 15952, 15966, TU 1210.

Cañada Zalaya: Mao Formation: TU 1227A.

Stratigraphic distribution.—Gurabo and Mao Formations, Dominican Republic.

Geographic distribution.—Dominican Republic.

***Prunum conforme* (Sowerby, 1850)**

Plate 2, figures 1, 3, 6.

Marginella conformis Sowerby, 1850, pp. 45–46; Guppy, 1866, p. 288, pl. 17, fig 2; 1874, p. 440; Gabb, 1873, p. 221; Guppy, 1876, p. 528; Guppy and Dall, 1896, pp. 309–310; Dall, 1903, p. 1583; Maury 1917, p.234, pl. 37, figs. 5, 5a; Pilsbry, 1922, pp. 337–338; Woodring, 1928, pp 238–239, pl. 14, figs. 8, 9.

Description (Table 1).—Shell medium sized (10–20 mm), obovate in shape (height/width <1.8 mm) with weakly domed shape in lateral view. Shell thick, weakly shouldered, with nearly involute spire (0–5% of shell height). Anterior sinus absent. Aperture narrow, with inner lip generally conforming to body whorl. Ventral surface of shell rounded and lacking flanging or flattening. No color pattern visible. Four columellar folds present throughout ontogeny, occupying greater than half of aperture. Anterior fold not expanded, but uniform in width and forming anterior margin of aperture. Canal absent posterior to forth columellar fold. Four columellar folds nearly uniformly spaced. In dorsal view, spire callus absent, but large lip attachment callus present. Small callus band also extends parallel to lip, although not as developed as in *Prunum gibsonsmithorum*. Complete callus ring absent. Large and

thick posterior sinus callus process present, but inner apertural callus ridge (along the body whorl) absent. Callus not filling columellar fold interspaces. Ventral surface of spire partially covered with callus. On ventral surface of body whorl, callus covering aperture margin completely with bilobate shape. Posterior callus lobe thicker than anterior lobe, containing crescent shaped callus ridge. Irregular denticulations present but not extending very far into aperture. Denticulations best developed in middle of inner lip. Lip triangular in cross section as a result of extensive thickening of inner lip. Strong lip crenulations and thick external varix present. Lip attaching at same level as spire and angling from the body whorl at about 90 degrees from the columellar axis.

Type material.— Holotype USNM, 113769. (Woodring 1928, p. 239 lists a different number). Figured in Plate 2, figure 3.

Type locality.—Dominican Republic (Sowerby, 1850). Following article 72H (B) of the International Code of Zoological Nomenclature, a more specific type locality may be designated. The new type locality for *P. conforme* is hereby designated as the Río Gurabo section, Río Gurabo Formation, NMB locality 15860.

Material.—Measured and/or figured specimens: USNM 135340, USNM 113769, TU 1278. Other specimens are cataloged by locality and listed in the Occurrence section.

Comparisons.—*Prunum conforme* is easily distinguishable from other Dominican marginellids by (1) The presence of a bilobate aperture margin callus; (2) A posterior canal callus process; and (3) A crescent shaped callus ridge in the posterior callus lobe. In the upper Gurabo Formation (300–380 meters), however, a series of samples contain specimens morphologically intermediate between *P. conforme* and *P. christinelladae* (Nehm and Geary, 1994). Morphological and stratigraphic patterns observed in this interval indicate that *P. conforme* gives rise to *P. christinelladae* (see Nehm and Geary [1994] for a detailed discussion of this speciation event). *P. conforme* shares a similar size and overall shape with *P. aurorum* (Gardner) from the Chipola Formation of Florida. *P. aurorum* has more angular shouldering, a wider aperture, and different callus patterns than *P. conforme*.

Occurrence.—This species was collected from the following NMB and TU localities (see Stratigraphic Distribution, p. 9, and Saunders *et al.* [1986] for locality information):

Río Cana section: NMB localities 16857, 16864, 16865, 16866, 16867, 16868, 16869.

Río Gurabo section: NMB localities 15807, 15814, 15819, 15824, 15837, 15842, 15843, 15844, 15846,

15847, 15848, 15857, 15858, 15859, 15860, 15861, 15863, 15864, 15865, 15866, 15867, 15868, 15869, 15870, 15871, 15875, 15897, 16808, 16809, 16810.

Río Mao section: NMB locality 16801.

Río Yaque del Norte section at López: NMB locality 17282.

Río Yaque del Norte section at Arroyo López: NMB locality 17275.

Río Yaque del Norte section at La Barranca: NMB locality 17268.

Cañada Zalaya section: TU 1227A.

Stratigraphic distribution.—Upper Pliocene Bowden beds of Jamaica; Miocene Thomonde Formation of Haiti; Lower to Middle Miocene Baitoa Formation, Upper Miocene Cercado Formation, Lower Pliocene Gurabo Formation, Upper Pliocene Mao Formation, Dominican Republic.

Geographic distribution.—Jamaica, Haiti, Dominican Republic.

***Prunum domingoense* (Dall, 1896)**

Plate 2, figure 2.

Marginella domingoense Dall, 1896, p. 310; Maury 1917a, p. 236.

Original description.—"Oligocene of Santo Domingo, from an island in Lake Henriquillo, and also from the Potrero, Río Amina, Bland. This species is very close to *M. aurora*, Dall, from the Chipola Marl, but has the tip of the spire less conspicuous and the aperture quite flexuous instead of nearly straight." (Dall, 1896, p. 310).

Description (Table 1).—Shell medium sized (10–20 mm), obovate in shape (height/width <1.5 mm) with weakly domed shape in lateral view. Shell thick, weakly shouldered, with nearly involute spire (0–5% of shell height). Anterior sinus absent. Aperture narrow, with inner lip generally conforming to body whorl. Ventral surface of shell rounded, lacking flanging or flattening. No color patterns present. Four columellar folds present throughout ontogeny, occupying about half of aperture. Anterior fold does not expand, but is uniform in width, forming anterior margin of aperture. Canal not present posterior to fourth columellar fold. Four columellar folds nearly uniformly spaced. In dorsal view, spire callus absent, but lip attachment callus present. Small callus band extending parallel to lip, although not as developed as in *P. gibsonsmithorum*. Complete callus ring absent. A large and thick posterior sinus callus process is absent. Inner apertural callus ridge along body whorl absent. Callus not filling columellar fold interspaces. Ventral surface of spire not covered with callus. On ventral surface of body whorl callus covering complete aperture margin. Callus margin lacking any distinctive lobes. Irregular den-

ticulations poorly developed and not extending very far into the aperture. Lip is very thick and triangular in cross section. Lip crenulations absent. Thick external varix present. Lip attaches at same level as spire and angled from body whorl at about 90 degrees from columellar axis.

Type material.—Holotype USNM 113768. Figured in Plate 2, figure 2.

Type locality.—An island in Lake Henriquillo, southern Santo Domingo (Dall, 1896).

Material.—Measured and/or figured specimens: USNM 113768.

Measurements.—Holotype: Height 24.3 mm.

Remarks.—It is unlikely that this species occurs in the Neogene of the Cibao Valley.

Occurrence.—This species was not collected from any NMB or TU localities and probably does not occur in the Neogene formations of the Cibao Valley.

Stratigraphic distribution.—?Neogene, Dominican Republic.

Geographic distribution.—Dominican Republic.

***Prunum gibsonsmithorum*, new species**

Plate 3, figures 1, 3.

Description (Table 1).—Shell large (20–30 mm), cylindrical in shape (height/width >1.8 mm) with weakly domed shape in lateral view. Shell thick, weakly shouldered, with short spire (5–10% of shell height). Anterior sinus absent. Aperture very narrow and constricted, with inner lip conforming to body whorl. Ventral surface of shell rounded, lacking flanging or flattening. No color pattern visible, although the specimens available have worn surfaces. Four columellar folds present, restricted to anterior ¼ of aperture. Anterior fold does not expand, but is uniform in width, forming anterior aperture wall. Canal not present posterior to fourth columellar fold (as may be observed in *P. latissimum*). Four columellar folds nearly uniformly spaced. In dorsal view, spire callus visible, as is lip attachment callus. Callus band also extending parallel to lip, although not developed into complete callus ring (as observed in *P. marginatum*). Posterior sinus callus process absent, but inner apertural callus ridge present along body whorl. Callus fills columellar fold interspaces. Ventral surface of spire nearly covered with callus. On ventral surface of body whorl, callus covers aperture margin completely. Very small, irregular denticulations not extending into aperture. Denticulations occupying middle of inner lip. Lip triangular in cross section due to extensive thickening of inner lip. Strong lip crenulations absent; external varix present. Lip attaching below spire and angled from body whorl at over 135 degrees from columellar axis.

Type material.—Holotype NMB H 18107; Paratype NMB H 18108; Figured in Plate 3, figure 1, 3.

Type locality.—TU 1354 (Gurabo Formation, Cañada de Zamba, Río Cana) see Saunders *et al.* (1986, p. 66).

Material.—Measured and/or figured specimens: TU 1354, NMB locality 16818.

Measurements.—Holotype: Height, 28.6 mm, width 13.7 mm.

Comparisons.—*Prunum gibsonsmithorum* shares many morphological features with the extinct species *P. limonensum* (Dall, 1896), *P. willcoxianum* (Dall, 1890), and *P. prewillcoxianum* (Perrilliat, 1973) and the extant species *P. carneum* (Storer, 1837) and *P. roosevelti* (Bartsch and Rehder, 1939): (1) a callus that fills the columellar fold interspaces; (2) a callus that covers the ventral surface of the spire; and (3) a ventral callus that covers the complete aperture margin. *Prunum prewillcoxianum* from the Pliocene of Mexico has a shorter spire, a flat spire shelf, a thick and massive ventral callus deposit near the anterior end of the shell, and a callus on the ventral anterior surface that projects out from the body whorl in aperture view. *Prunum willcoxianum* from the Pliocene of Florida is smaller, has a strong bend and ridge in the posterior body whorl and an apex callus that covers the entire spire in dorsal view. *Prunum limonensum* from the Pliocene and Pleistocene of Costa Rica is significantly larger, and the callus obscures only half of the spire in dorsal and ventral view. In addition, the outer lip of *P. limonensum* does not closely conform to the body whorl. The Recent western Atlantic species *P. carneum* and *P. roosevelti* are shorter, stouter, and have straighter outer lips.

Remarks.—Ecological knowledge is lacking for many of the members of this lineage. It is thought that *Prunum limonensum* inhabited lagoonal environments in the Limon Basin of Costa Rica (Robinson, 1991), much like the extant species *P. carneum*, which is known from shallow water carbonate environments and *Halimeda* beds (personal observation 1994). It is difficult to determine the paleoenvironmental preferences of *P. gibsonsmithorum* because only two specimens are available for study.

Occurrence.—This species was collected from the following NMB and TU localities (see Stratigraphic Distribution, p. 9, and Saunders *et al.* [1986] for locality information): Río Cana, Gurabo Formation: TU 1354, NMB locality 16818.

Stratigraphic range.—Gurabo Formation, Dominican Republic.

Geographic range.—Dominican Republic.

Etymology of name.—Named in honor of Jack and Winifred Gibson-Smith in recognition of their contri-

butions to Caribbean malacology. Their extensive collections have greatly enhanced our understanding of the systematics and evolution of *Prunum* species.

***Prunum latissimum* (Dall, 1896)**

Plate 1, figures 4, 5, 10.

Marginella latissimus Dall, 1896, p. 308, pl. 29, fig. 11; Maury, 1917a, p.236.

Original description.—"Shell small, very solid and broad, externally smooth and polished, a wash of callus obscuring a very low spire of about 3 whorls; base callous; outer lip broad, thick, with a groove behind it and a low callus on the shoulder behind the groove; aperture narrow, the outer lip smoother in front and behind, minutely denticulate near the middle; inner lip thickened; body with two transverse plait, the posterior smaller; pillar short, with two oblique plait, the anterior smaller. Lon. Of shell 11, lat. 8.5 mm." (Dall, 1896, p. 308).

Description (Table 1).—Shell small (< 10 mm), very obovate in shape (height/width <1.5mm), strongly domed in lateral view. Shell very thick, weakly shouldered, with short spire (5–10% of shell height). Anterior sinus absent. Aperture narrow, with inner lip generally conforming to body whorl. Ventral surface of shell very rounded, lacking flanging or flattening. Color pattern visible: two widely spaced thin stripes present on body whorl. Four columellar folds present throughout ontogeny, occupying more than half of aperture. Anterior fold expands anteriorly forming ridge. Conspicuous canal present posterior to fourth columellar fold. Four columellar folds not uniformly spaced: anterior two folds nearly touch one another but posterior folds are widely spaced. In dorsal view, spire callus absent, but lip attachment callus present. Very small callus band also extends parallel to lip. Complete callus ring absent. Posterior sinus callus process present, but inner apertural callus ridge absent along body whorl. Callus does not fill columellar fold interspaces. Ventral surface of spire partially covered with callus. Callus covers complete aperture margin on ventral surface of body whorl. Posterior margin callus contains very thick process extending into aperture. Irregular denticulations present on lip, but not extending into aperture. Denticulations best developed in middle of inner lip. Lip triangular in cross section. Strong lip crenulations absent. External varix present and very thick. Lip attaches below spire, angling from the body whorl at about 80 degrees from columellar axis.

Type material.—Holotype: USNM 113740. Figured in Plate 1, figure 5.

Type locality.—Erroneously reported to occur in the Pliocene clays of Moen, Costa Rica (Dall, 1896).

Material.—Measured and/or figured specimens: USNM 113740, NMB localities 17286, 17288. Other specimens are cataloged by locality and listed in the Occurrence section.

Measurements.—Holotype: 11 mm height, width 8.5 mm.

Comparisons.—*Prunum latissimum* is very similar to *P. eleutherium dasum* (Gardner) from the Miocene Chipola Formation of Florida. *Prunum dasum* lacks the two body whorl stripes present on *P. latissimum*. In addition, there are slight differences in the thickness, area, and shape of the posterior sinus callus process between the two species.

Remarks.—Robinson (1991) notes that he did not find any specimens of this species in the Moin Formation of Costa Rica, which is the type locality according to Dall (1896). He notes that “this species may be found in the Río Banano Formation” but he never collected any specimens in the Río Banano Formation (Robinson, 1991). Extensive collections of fossil material by members of the Panama Paleontology Project (PPP) include numerous samples from the Río Banano Formation (Coates *et al.*, 1992). Study of this material has not turned up any specimens of *P. latissimum* (Nehm, unpublished data). It is likely that Dall’s material was from the Dominican Republic or Haiti and that *P. latissimum* does not occur in Costa Rica.

Occurrence.—This species was collected from the following NMB and TU localities (see Stratigraphic Distribution, p. 9, and Saunders *et al.* [1986] for locality information):

Río Yaque del Norte (López) TU 1363, 1364; NMB localities 16935, 16936, 16938, 16940, 16942, 16945, 17265, 17275, 17280, 17282, 17283, 17284, 17286, 17287, 17288, 17289, 17290, 17290.

Stratigraphic distribution.—Lower to Middle Miocene Baitoa Formation, Dominican Republic; Miocene Thomonde Formation, Haiti.

Geographic distribution.—Haiti, Dominican Republic.

***Prunum maoense* (Maury, 1917a)**

Plate 1, figures 7, 8, 11

Marginella maoense Maury, 1917a, p. 235, pl. 11, fig. 7.

Original description.—“Shell oblong-ovate, resembling *M. apicina* Menke in form, but about half as large, with a slightly more prominent spire, and with the body-whorl convex, not medially contracted as in *apicina*. Whorls four, suture obscure; aperture narrow, widening outer lip heavily thickened except anteriorly, closely and finely crenulate within; columella with four plications, the two anterior stronger, longer,

oblique, the two posterior weaker, nearly transverse. Color pattern consisting of two narrow, well-defined dark-gray bands, one almost central, the other anterior, thus dividing the body whorl into three subequal zones; no spots are present. Length 10, width 6 mm.” (Maury, 1917a, p. 235).

Description (Table 1).—Shell small (< 10 mm), ob-ovate in shape (height/width < 1.8 mm) with weakly domed shape in lateral view. Shell thick, weakly shouldered, with short spire (5–10% of shell height). Anterior sinus absent. Aperture narrow, with inner lip generally conforming to body whorl. Ventral surface of shell lacking flanging or flattening. Color pattern visible: two widely spaced thin stripes present on body whorl. Four columellar folds present throughout ontogeny, occupying more than half of aperture. In some specimens anterior fold expands to form ridge. Canal absent posterior to forth columellar fold. Four columellar folds not uniformly spaced: anterior two folds closer together than posterior two folds. In dorsal view, spire callus absent, but lip attachment callus present. Very small callus band extends parallel to lip. Complete callus ring absent. Posterior sinus callus process and inner apertural callus ridge absent along body whorl. Callus not filling columellar fold interspaces. Ventral surface of spire not covered with callus. On ventral surface of body whorl, callus covering most of aperture margin. Irregular denticulations present, but not extending into aperture. Denticulations best developed in middle of inner lip. Lip triangular in cross section. Strong lip crenulations absent. External varix present. Lip attaches below spire and angled from body whorl at about 80 degrees from columellar axis.

Type material.—The holotype of *Prunum maoense* (PRI 28683) is lost (Wendy Taylor, pers. comm. 1994). Following Article 74 (C) of the International Code of Zoological Nomenclature (1985) a neotype (NMB H 18112) is designated as a replacement of Maury’s holotype. This adult specimen is from NMB locality 16839 from the Río Cana section, Upper Miocene Cercado Formation.

Type locality.—Cercado Formation, Bluff 3, Río Mao, Dominican Republic.

Material.—Measured and/or figured specimens: NMB locality 16839; TU 1354; TU 1449. Other specimens are cataloged by locality and listed in the Occurrence section.

Measurements.—Holotype: Length 10 mm, width 6 mm (Maury, 1917a). Neotype (NMB H 18112): Length 7.2 mm.

Comparisons.—*Prunum maoense* is a small species that demonstrates considerable morphological variation. It is differentiated from the smaller *P. mauryense* by denticulations, a prominent outer lip varix, and the

presence of two color bands on the body whorl. *Prunum maoense* is difficult to distinguish from *P. latissimum*, but in general the shell of *P. latissimum* has heavier callusing and a more prominent callus process on the posterior aperture margin. These two species appear to be a single evolving lineage (Nehm, 1998).

Occurrence.—This species was collected from the following NMB and TU localities (see Biostratigraphy, p. 9, and Saunders *et al.* [1986] for locality information):

Río Cana section: NMB localities 16817, 16818, 16820, 16828, 16834, 16835, 16836, 16837, 16838, 16839, 16842, 16843, 16844, 16848, 16852, 16857, 16879, 16977, 16984, 16986, 16989, 16995, 17005.

Río Gurabo section: NMB localities 15836, 15873, 15878, 15881, 15882, 15897, 15900, 15902, 15903, 15904, 15905, 15906, 15907, 15908, 15910, 15911, 15912, 15913, 15914, 15919.

Río Mao section: NMB localities 16910, 16913, 16914, 16915, 16916, 16918, 16923, 16924, 16926, 16927, 16928, 16929, 16932.

Stratigraphic distribution.—Upper Miocene Cerredo Formation, Lower Pliocene Gurabo Formation, Dominican Republic; Miocene Thomande Formation, Haiti; Upper Pliocene Bowden Formation, Jamaica.

Geographic distribution.—Dominican Republic, Haiti, Jamaica.

***Prunum mauryense*, new species**

Plate 3, figures 4–6.

Description (Table 1).—Shell very small (<5 mm), cylindrical in shape (height/width >1.8 mm) with very weakly domed shape in lateral view. Shell thin, weakly shouldered, with tall spire (10%–20% of shell height). Spire very broad and smooth; sutures not clearly visible. Anterior sinus absent. Aperture narrow, conforming to shape of body whorl. Ventral surface of shell slightly rounded lacking flanging or flattening. No color pattern visible. Four columellar folds present occupying less than half of aperture. Anterior fold does not expand, but is uniform in width, forming weak rim at anterior margin of aperture. Canal not present pos-

terior to fourth columellar fold. Four columellar folds nearly uniformly spaced. In dorsal view, both spire callus and large lip attachment callus absent. Small callus band parallel to lip and posterior sinus callus process also absent, as is inner apertural callus ridge along body whorl. Callus not filling columellar fold interspaces. Ventral surface of spire not covered with callus. On ventral surface of body whorl callus restricted to columellar fold area. Outer lip bulges out medially, constricting anteriorly. Denticulations absent, lip nearly straight in cross section. Lip crenulations absent but very weak external varix present. Lip attaches below spire and angled from body whorl at about 90 degrees from columellar axis.

Type material.—Holotype: NMB H 18109; Paratypes: NMB H 18110; NMB H 18111. Figured in Plate 3, figures 4–6.

Type locality.—TU 1227A, Mao Formation, Cañada Zalaya, Dominican Republic (Saunders *et al.*, 1986, p. 65).

Material.—Measured and/or figured specimens: Plate 3, figures 4–6. TU 1227A.

Measurements.—Holotype: height 4.8 mm, width 2.1 mm.

Remarks.—*Prunum mauryense* is similar morphologically to *P. bellum tersum* (Mansfield, 1930), *P. bellum hosfordensis* (Mansfield, 1930), *P. succinea* (Conrad, 1846), and *P. avenellum* (Dall, 1881). These species share a cylindrical shell shape, the absence of extensive callus, and very tall spires. *Prunum mauryense* is smaller and has a wider spire than these other species.

Occurrence.—This species was collected from the following NMB and TU localities (see Saunders *et al.*, 1986 for locality information): Cañada Zalaya section: TU 1227A.

Stratigraphic distribution.—Upper Pliocene Mao Formation, Cañada Zalaya, Dominican Republic.

Geographic distribution.—Dominican Republic.

Etymology of name.—Named in honor of Dr. Carlotta Maury for her work on the Neogene paleontology of the Dominican Republic.

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APPENDIX

Sample data, including source institution, sample number, species, formation, and location in each section.

Species	River section	Sample	Formation	Meters	n
<i>aminum</i>	Lopez	16936	Baitoa	42	3
<i>aminum</i>	Lopez	1363	Baitoa	n/a	2
<i>aminum</i>	Lopez	1364	Baitoa	n/a	1
<i>christineladdae</i>	Gurabo	15837	Gurabo	375	3
<i>christineladdae</i>	Gurabo	15809	Gurabo	382	14
<i>christineladdae</i>	Gurabo	15952	Gurabo	384	1
<i>christineladdae</i>	Gurabo	15807	Gurabo	388	11
<i>christineladdae</i>	Gurabo	15810	Gurabo	392	11
<i>christineladdae</i>	Gurabo	15806	Gurabo	392	2
<i>christineladdae</i>	Gurabo	15805	Gurabo	396	45
<i>christineladdae</i>	Gurabo	15811	Gurabo	396	23
<i>christineladdae</i>	Gurabo	15812	Gurabo	396	1
<i>christineladdae</i>	Gurabo	15803	Gurabo	397	18
<i>christineladdae</i>	Gurabo	15813	Gurabo	400	6
<i>christineladdae</i>	Gurabo	15816	Gurabo	401	25
<i>christineladdae</i>	Gurabo	15966	Gurabo	404	3
<i>christineladdae</i>	Gurabo	15817	Gurabo	405	16
<i>christineladdae</i>	Gurabo	15818	Gurabo	411	2
<i>christineladdae</i>	Gurabo	15820	Gurabo	419	2
<i>christineladdae</i>	Gurabo	1210	Gurabo	n/a	50+
<i>gibsonsmithorum</i>	Cana	16818	Gurabo	346	1
<i>gibsonsmithorum</i>	Cana	1354	Gurabo	n/a	1
<i>latissimum</i>	Arroyo Lopez	17275	Cercado?	n/a	1
<i>latissimum</i>		17280	Baitoa		8
<i>latissimum</i>	Lopez	17282	Baitoa	7	2
<i>latissimum</i>	Lopez	16945	Baitoa	9	3
<i>latissimum</i>	Lopez	17284	Baitoa	9	4
<i>latissimum</i>	Lopez	17283	Baitoa	13	56
<i>latissimum</i>	Lopez	17286	Baitoa	23	248
<i>latissimum</i>	Lopez	17287	Baitoa	27	62
<i>latissimum</i>	Lopez	17288	Baitoa	29	81
<i>latissimum</i>	Lopez	17289	Baitoa	31	14
<i>latissimum</i>	Lopez	17290	Baitoa	34	13
<i>latissimum</i>	Lopez	16935	Baitoa	38	48
<i>latissimum</i>	Lopez	16936	Baitoa	42	81
<i>latissimum</i>	Lopez	17265	Baitoa	42	9

APPENDIX

Continued.

Species	River section	Sample	Formation	Meters	n
<i>latissimum</i>	Lopez	16938	Baitoa	46	33
<i>latissimum</i>	Lopez	16940	Baitoa	49	18
<i>latissimum</i>	Lopez	16942	Baitoa	51	16
<i>latissimum</i>	Lopez	1363	Baitoa	n/a	>10
<i>latissimum</i>	Lopez	1364	Baitoa	n/a	>10
<i>coniforme</i>	Cana	16857	Cercado	149	1
<i>coniforme</i>	Cana	16818	Gurabo	345	2
<i>coniforme</i>	Cana	16864	Gurabo	414	3
<i>coniforme</i>	Cana	16866	Gurabo	427	14
<i>coniforme</i>	Cana	16867	Gurabo	428	8
<i>coniforme</i>	Cana	16865	Gurabo	431	7
<i>coniforme</i>	Cana	16868	Gurabo	438	7
<i>coniforme</i>	Cana	16869	Gurabo	547	2
<i>coniforme</i>	Gurabo	15897	Cercado	137	1
<i>coniforme</i>	Gurabo	15875	Gurabo	209	1
<i>coniforme</i>	Gurabo	15870	Gurabo	219	1
<i>coniforme</i>	Gurabo	15871	Gurabo	221	12
<i>coniforme</i>	Gurabo	16809	Gurabo	221	7
<i>coniforme</i>	Gurabo	15865	Gurabo	222	17
<i>coniforme</i>	Gurabo	16810	Gurabo	222	10
<i>coniforme</i>	Gurabo	16808	Gurabo	223	4
<i>coniforme</i>	Gurabo	15867	Gurabo	223	3
<i>coniforme</i>	Gurabo	15868	Gurabo	223	2
<i>coniforme</i>	Gurabo	15869	Gurabo	224	1
<i>coniforme</i>	Gurabo	15864	Gurabo	225	24
<i>coniforme</i>	Gurabo	15866	Gurabo	227	2
<i>coniforme</i>	Gurabo	15863	Gurabo	236	17
<i>coniforme</i>	Gurabo	15860	Gurabo	255	23
<i>coniforme</i>	Gurabo	15858	Gurabo	276	1
<i>coniforme</i>	Gurabo	15857	Gurabo	276	2
<i>coniforme</i>	Gurabo	15847	Gurabo	280	1
<i>coniforme</i>	Gurabo	15848	Gurabo	281	3
<i>coniforme</i>	Gurabo	15846	Gurabo	287	9
<i>coniforme</i>	Gurabo	15844	Gurabo	312	3
<i>coniforme</i>	Gurabo	15843	Gurabo	312	8
<i>coniforme</i>	Gurabo	15842	Gurabo	314	28
<i>coniforme</i>	Gurabo	15837	Gurabo	375	3
<i>coniforme</i>	Gurabo	15807	Gurabo	388	6
<i>coniforme</i>	Gurabo	15814	Gurabo	404	2
<i>coniforme</i>	Gurabo	15819	Gurabo	414	1
<i>coniforme</i>	La Barranca	17268	Gurabo	n/a	1
<i>coniforme</i>	Lopez	17282	Baitoa	42	1
<i>coniforme</i>	Arroyo Lopez	17275	Cercado	n/a	1
<i>coniforme</i>	Mao	16801	Cercado?	n/a	1
<i>coniforme</i>	Zalaya	1227A	Mao	n/a	100+
<i>maoense</i>	Cana	16857	Cercado	149	23
<i>maoense</i>	Cana	16995	Cercado	223	3
<i>maoense</i>	Cana	16842	Cercado	228	4
<i>maoense</i>	Cana	16843	Cercado	228	1
<i>maoense</i>	Cana	16844	Cercado	228	63
<i>maoense</i>	Cana	16848	Cercado	228	4
<i>maoense</i>	Cana	16852	Cercado	228	4
<i>maoense</i>	Cana	16989	Cercado	228	5
<i>maoense</i>	Cana	16839	Cercado	231	74
<i>maoense</i>	Cana	16986	Cercado	232	7
<i>maoense</i>	Cana	16838	Cercado	233	4
<i>maoense</i>	Cana	16838	Cercado	233	33

APPENDIX

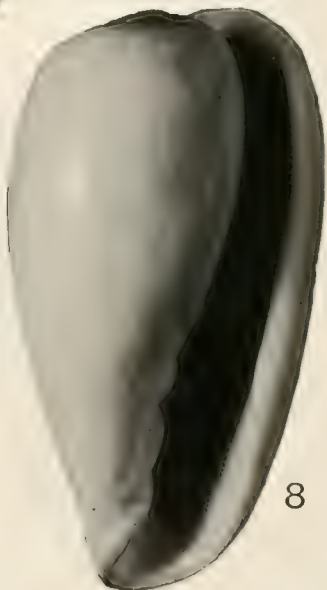
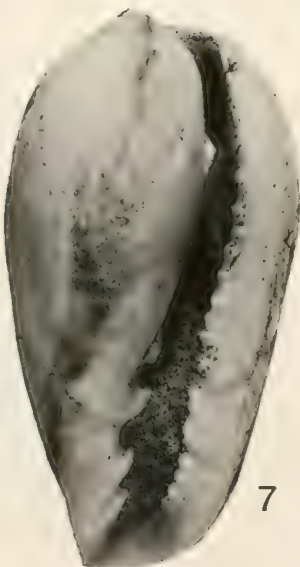
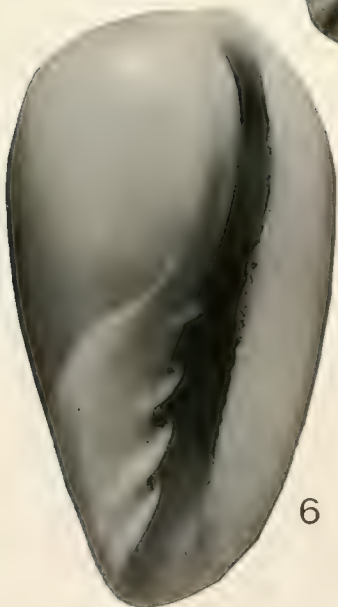
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Species	River section	Sample	Formation	Meters	n
<i>maoense</i>	Cana	16837	Cercado	237	51
<i>maoense</i>	Cana	16836	Cercado	240	6
<i>maoense</i>	Cana	16835	Cercado	252	25
<i>maoense</i>	Cana	16834	Gurabo	280	17
<i>maoense</i>	Cana	16977	Gurabo	300	4
<i>maoense</i>	Cana	16820	Gurabo	306	1
<i>maoense</i>	Cana	16828	Gurabo	309	40
<i>maoense</i>	Cana	16879	Gurabo	343	3
<i>maoense</i>	Cana	16817	Gurabo	346	14
<i>maoense</i>	Cana	16818	Gurabo	347	10
<i>maoense</i>	Gurabo	15919	Cercado	59	3
<i>maoense</i>	Gurabo	15914	Cercado	101	8
<i>maoense</i>	Gurabo	15913	Cercado	103	1
<i>maoense</i>	Gurabo	15912	Cercado	105	3
<i>maoense</i>	Gurabo	15911	Cercado	111	1
<i>maoense</i>	Gurabo	15910	Cercado	119	6
<i>maoense</i>	Gurabo	15908	Cercado	119	2
<i>maoense</i>	Gurabo	15903	Cercado	121	15
<i>maoense</i>	Gurabo	15900	Cercado	123	14
<i>maoense</i>	Gurabo	15902	Cercado	126	1
<i>maoense</i>	Gurabo	15904	Cercado	127	6
<i>maoense</i>	Gurabo	15907	Cercado	127	6
<i>maoense</i>	Gurabo	15905	Cercado	130	1
<i>maoense</i>	Gurabo	15906	Cercado	133	31
<i>maoense</i>	Gurabo	15897	Cercado	137	1
<i>maoense</i>	Gurabo	15882	Gurabo	186	16
<i>maoense</i>	Gurabo	15881	Gurabo	187	8
<i>maoense</i>	Gurabo	15878	Gurabo	195	46
<i>maoense</i>	Gurabo	15873	Gurabo	207	8
<i>maoense</i>	La Barraca	1449	Gurabo	n/a	1
<i>maoense</i>	Mao	16910	Cercado?	n/a	1
<i>maoense</i>	Mao	16913	Cercado?	n/a	5
<i>maoense</i>	Mao	16914	Cercado?	n/a	7
<i>maoense</i>	Mao	16915	Cercado?	n/a	2
<i>maoense</i>	Mao	16916	Cercado?	n/a	14
<i>maoense</i>	Mao	16918	Cercado?	n/a	5
<i>maoense</i>	Mao	16923	Cercado?	n/a	1
<i>maoense</i>	Mao	16924	Cercado?	n/a	22
<i>maoense</i>	Mao	16926	Cercado?	n/a	27
<i>maoense</i>	Mao	16927	Cercado?	n/a	7
<i>maoense</i>	Mao	16928	Cercado?	n/a	27
<i>maoense</i>	Mao	16929	Cercado?	n/a	3
<i>maoense</i>	Mao	16932	Cercado?	n/a	76
<i>mauryense</i>	Zalaya	1227A	Mao	n/a	1000+

EXPLANATION OF PLATE 1

Figure	Page
1-3. Prunum apicinum (Menke, 1828).	21, 26
All specimens from locality RHN 194: Florida Keys, USA; Recent.	
1. Adult. Height, 10.2 mm.	
2. Juvenile. Height, 7 mm.	
3. Late-stage juvenile. Height, 8.5 mm.	
4, 5, 10. Prunum latissimum (Dall, 1896).	36
4. NMB locality 17288: López, Dominican Republic; Baitoa Formation, Lower to Middle Miocene. Adult specimen. Height, 9.4 mm.	
5. Holotype. USNM 113740. Moen, Costa Rica; Pliocene (in error?). Adult specimen. Height, 10.9 mm.	
10. NMB locality 17286: López, Dominican Republic; Baitoa Formation, Lower to Middle Miocene. Adult specimen. Height, 12.1 mm.	
6. Prunum eleutherium dasum (Gardner, 1928).	37
6. TU locality 820B: Florida, USA; Chipola Formation, Lower to Middle Miocene. Adult specimen. Height 11.3 mm.	
7, 8, 11. Prunum maoense (Maury, 1917).	37
7. Neotype. NMB H 18112. NMB locality 16839: Río Cana; Upper Miocene Cercado Formation. Adult specimen. Height, 7.2 mm.	
8. TU locality 1449: Río Yaque del Norte, La Barranca; Upper Miocene part of Gurabo Formation. Adult specimen. Height, 6.8 mm.	
11. TU locality 1354: Río Cana, Cañada de Zamba; Upper Miocene part of Cercado Formation. Adult specimen. Height, 9.7 mm.	
9. Prunum aurorum (Gardner, 1928).	34
9. TU locality 950: Florida, USA; Chipola Formation; Lower to Middle Miocene. Adult specimen. Height, 24.9 mm.	



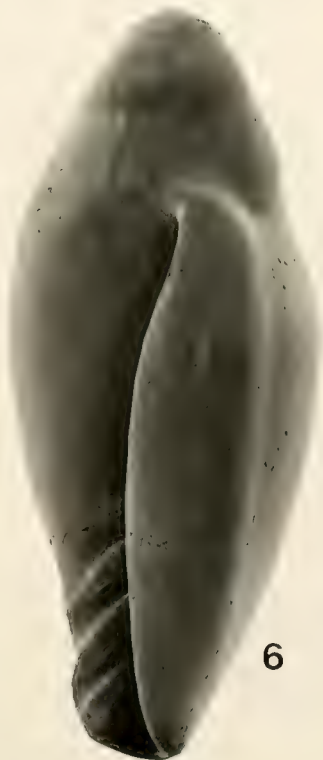
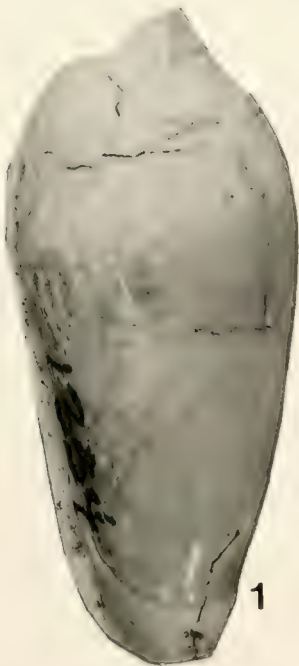


EXPLANATION OF PLATE 2

Figure	Page
1, 3, 6. <i>Prunum coniforme</i> (Sowerby, 1849).	34
1. USNM 135340: Bowden, Jamaica; Bowden Formation, Lower Pliocene. Adult specimen. Height, 20.6 mm.	
3. Holotype. USNM 113769: Potrero, Río Amina, Santo Domingo, Dominican Republic. Adult specimen. Height, 20.8 mm.	
6. TU locality 1278: Río Gurabo, Dominican Republic; Lower Pliocene part of Gurabo Formation. Adult specimen. Height, 26.5 mm.	
2. <i>Prunum domingoense</i> (Dall, 1896).	35
2. Holotype. USNM 113768: Potrero, Río Amina, Santo Domingo, Dominican Republic. Adult specimen. Height, 24.3 mm.	
4, 8. <i>Prunum christineladdae</i> (Maury, 1917).	33
4. Holotype. PRI 28682: Río Gurabo at Los Quemados, Dominican Republic. Adult specimen. Height, 19.3 mm.	
8. NMB locality 15818: Río Gurabo, Dominican Republic; Lower Pliocene part of Gurabo Formation. Adult specimen. Height, 16.0 mm.	
5, 7. <i>Prunum aminum</i> (Dall, 1896).	32
5. Holotype. USNM 113773: Potrero, Río Amina, Santo Domingo, Dominican Republic. Adult specimen. Height, 25.5 mm.	
7. NMB locality 16936: López, Dominican Republic; Baitoa Formation, Lower to Middle Miocene. Adult specimen. Height, 25.2 mm.	

EXPLANATION OF PLATE 3

Figure	Page
1, 3. <i>Prunum gibsonsmithorum</i> , new species.	35
1. Holotype. NMB H 18107. TU locality 1354: Río Cana, Cañada de Zamba; Upper Miocene part of Cercado Formation. Adult specimen. Height, 28.6 mm.	
3. Paratype. NMB H 18108. NMB locality 16818: Río Cana; Upper Miocene part of Gurabo Formation. Adult specimen. Height, 26.7 mm.	
2. <i>Prunum limonense</i> (Dall, 1896)	32, 36
2. NMB locality 18079: Limón, Costa Rica. Pliocene, Río Banano Formation. Adult specimen. Height, 33.2 mm.	
4-6. <i>Prunum mauryense</i> , new species.	38
4. Holotype. NMB H 18109. TU locality 1227A: Cañada Zalaya, Dominican Republic; Lower Pliocene Mao Formation. Adult specimen. Height, 4.8 mm.	
5. Paratype. NMB H 18110. TU locality 1227A: Cañada Zalaya, Dominican Republic; Lower Pliocene Mao Formation. Adult specimen. Height, 4.7 mm.	
6. Paratype. NMB H 18111. TU locality 1227A: Cañada Zalaya, Dominican Republic; Lower Pliocene Mao Formation. Adult specimen. Height, 4.7 mm.	



NEOGENE PALEONTOLOGY IN THE NORTHERN DOMINICAN REPUBLIC 22 THE FAMILY NERITIDAE (MOLLUSCA: GASTROPODA)

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ABSTRACT

Five species of neritid gastropods assigned to three genera occur in the Neogene formations of the Yaque Group of the Cibao Valley: *Nerita fulgurans* Gmelin, 1791; *Neritina figulopicta* Maury, 1917; *Neritina dominicana*, n. sp.; *Neritina jungi*, n. sp.; and *Smaragdia viridis* (Linnaeus, 1758). Approximately 111 samples studied from the Río Cana, Río Gurabo, Río Mao, and Río Yaque del Norte sections contain more than 1300 neritid specimens. *Nerita fulgurans* is rare and occurs in one sample in the Mao formation of the Río Gurabo. *Neritina figulopicta* is abundant and occurs in the Cercado and Gurabo Formations of the Río Cana, the Cercado and Gurabo Formations of the Río Mao, and the Baitoa Formation of the Río Yaque del Norte at López. *Neritina dominicana* is rare and is restricted to the Cercado Formation of the Río Cana section. *Neritina jungi* is also rare and occurs in the Cercado Formation of the Río Cana and the Gurabo Formation of the Río Gurabo. *Smaragdia viridis* is the most abundant Dominican neritid and occurs in the Cercado and Gurabo formations of the Río Cana, the Cercado and Gurabo formations of the Río Gurabo, the Cercado and Gurabo formations of the Río Mao, and the Baitoa Formation of the Río Yaque del Norte at López.

Neritid genera have restricted environmental ranges and ecological associations, and therefore have great potential as paleoenvironmental and paleoecological indicators in the fossil record. Specifically, the presence, abundance, and distribution of *Smaragdia* species, which are obligatory seagrass epibionts, provide strong evidence for the presence and distribution of seagrasses in the Neogene of the Cibao Valley even though no seagrasses are preserved in the fossil record of this region. In addition, the presence, abundance, and distribution of *Neritina* species, which are commonly restricted to freshwater and/or brackish-water habitats, provide evidence for the presence and distribution of brackish paleoenvironments.

The presence, distribution, and abundance of *Smaragdia viridis* in the Río Cana, Río Gurabo, Río Mao, and López sections suggest that seagrass beds were geographically and stratigraphically widespread in the Neogene of the Dominican Republic. The distribution and abundance of *Neritina* specimens in the Río Cana, Río Gurabo, and Río Mao sections suggest that brackish conditions were also geographically widespread but stratigraphically limited. The distributions of *Smaragdia* and *Neritina* generally conform to previous paleoenvironmental reconstructions using ostracods, mollusks, and corals, but notable exceptions occur.

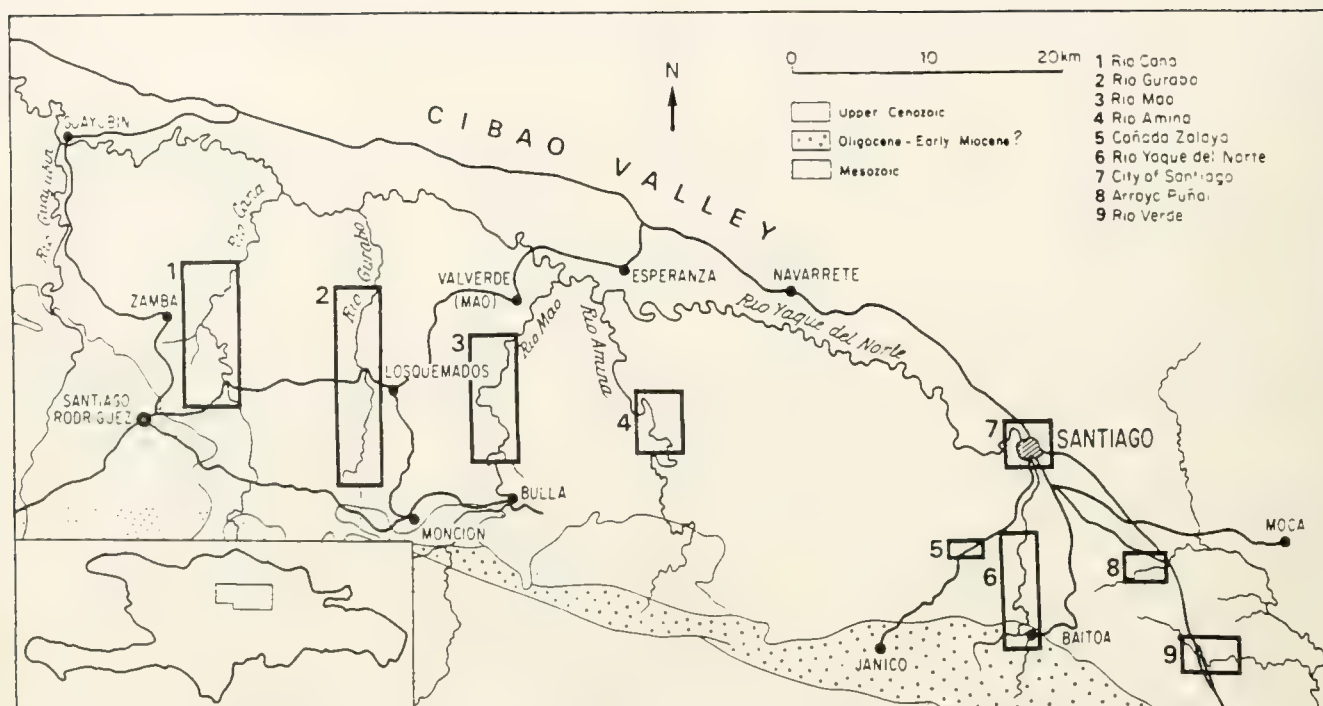
In the Río Cana section, *Smaragdia viridis* occurs from about 140 m to 380 m but is most abundant from 220 m to 260 m. This interval also contains grass-flat coral communities and seagrass-associated limpets. In the Río Cana section, *Neritina figulopicta* occurs from about 150 m to 250 m but is most abundant from 220 m to 230 m; it is most abundant in a stratigraphic interval containing beds of brackish-water bivalves and ostracods. In the Río Gurabo section, *S. viridis* occurs from about 80 m to 275 m but is most abundant from 100 m to 210 m. In the Río Gurabo section the stratigraphic range of *S. viridis* is much broader than that of seagrass-associated limpets. The interval of greatest abundance of *S. viridis* (100 m to 140 m) is discordant with the distribution of grass-flat corals. In the Río Gurabo section, *N. figulopicta* occurs from about 40 m to 130 m but is most abundant from about 40 m to 60 m. This interval also contains brackish water ostracods. The abundance and broad distribution of *S. viridis* and the rarity of *N. figulopicta* (three specimens) in the Baitoa section at López suggest shallow normal marine conditions and seagrass beds.

INTRODUCTION

This paper examines the fossil neritid gastropods of the Neogene of the northern Dominican Republic and contributes to a series of systematic, biostratigraphic, paleoecological, and evolutionary studies of the richly fossiliferous sediments of the Cibao Valley within the geological framework detailed by Saunders *et al.* (1982, 1986) (Text-fig. 1). This is the first family-level treatment of the Dominican “archaeogastropods,” and it illuminates the paleobiology of a diverse gastropod group that is otherwise poorly represented in the fossil record (Scott and Kenny, 1998).

Although species diversity is not high, the study of Dominican neritids is important for several reasons:

(1) Neritid genera are specialized in their ecological and environmental associations and therefore are useful as paleoecological and paleoenvironmental indicators in the Neogene sections of the Dominican Republic. In particular, *Smaragdia* and *Neritina* are strongly indicative of seagrass communities and brackish-water paleoenvironments, respectively. (2) Although neritids are rarely preserved as fossils (Scott and Kenny, 1998), their preservation and abundance are outstanding in the Dominican Republic. Dominican fossil species retain their original shell pigments and a variety of color pattern morphs in more than one thousand specimens. (3) Dominican neritids provide a unique opportunity to analyze the evolution of color



Text-figure 1.—Map of the Cibao Valley, northern Dominican Republic, showing collecting localities. Material for this study was collected from the five river sections listed at top right and shown in boxes. From Saunders *et al.* (1986).

polymorphism over macroevolutionary time (Costa *et al.*, 1998).

Modern publications on fossil mollusks increasingly have emphasized high-quality illustrations of coated specimens (ammonium chloride, gold palladium, platinum, etc.); photography is used for large shells (>5 mm) and scanning electron micrography is used for minute shells (<5 mm). The common neritid species in the Neogene of the Dominican Republic present a special challenge. Most specimens are minute (<5 mm) but coating is not an option because it obscures shell pigmentation patterning, which is an important morphological feature for systematic and evolutionary consideration. The intricate details of color patterns must be studied with a light microscope, and therefore *camera lucida* drawings are the most satisfactory method of illustration.

As in previous papers in this series, the reader is referred to the introductory volume by Saunders *et al.* (1986) for background data on the Dominican Republic Project and for detailed data on the stratigraphy, lithology, environment of deposition, age, and collecting localities.

ACKNOWLEDGMENTS

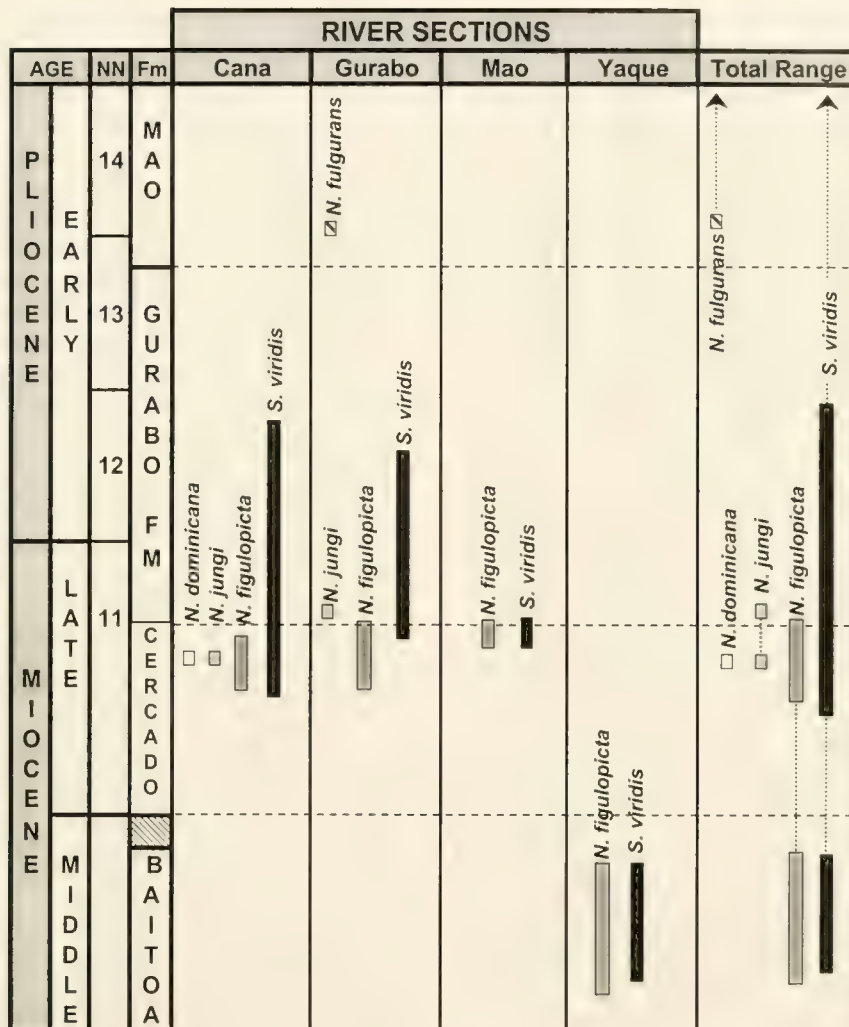
We thank Peter Jung, Naturhistorisches Museum, Basel, for the opportunity to participate in the Dominican Republic Project.

The material described herein was collected between 1978 and 1980 with the financial support of the Swiss National Science Foundation (Grant 2.646-0.76). We also thank Emily H. Vokes for her generous hospitality during a visit to Tulane University, and for providing extensive fossil material from the Vokes collections. FHAC acknowledges assistance with literature from Rudolph Scheltema. Financial support to RHN was provided by the National Science Foundation (Dissertation Improvement Grant), the Geological Society of America, Sigma Xi Grants in Aid of Research, and the Hawaiian Malacological Society. CSH is grateful to Catherine Unabia for discussions of neritoidean biology and problems of suprageneric classification and the University of California Museum of Paleontology and the University of California, Berkeley, Committee on Research for financial support. E. Vokes and G. Vermeij provided helpful reviews. This is Publication Number 1689 of the University of California Museum of Paleontology.

ABBREVIATIONS OF REPOSITORY INSTITUTIONS

The following abbreviations for repository institutions are used in this paper:

MORG: Fundação Universidade do Rio Grande, Rios Collection, Brazil.



Text-figure 2.—Stratigraphic distributions of Dominican neritid species from the Yaque Group of the Cibao Valley. River sections are labeled at the top (from west to east). Neogene Nannofossil (NN) zones are listed at the left and correlated with the Cercado, Gurabo, and Mao Formations. The Baitoa Formation has not been dated using planktonic foraminifera, but it is thought to be of lower or middle Miocene age based on biostratigraphic data from ostracods and molluscs (Saunders *et al.* [1986] and Vokes [1979]). See Text-figure 1 for geographic locations of the River sections. Stratigraphic and biostratigraphic information from Saunders *et al.* (1986). The overall stratigraphic distributions of neritid species from NMB samples. Stratigraphic correlations after Saunders *et al.* (1986, p. 35).

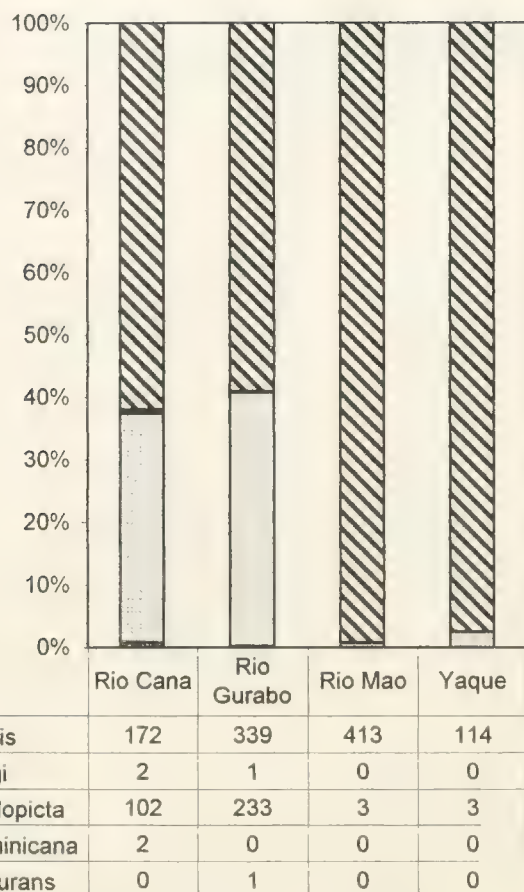
- NMB: Naturhistorisches Museum Basel, Switzerland.
 PRI: Paleontological Research Institution, Ithaca, NY, U.S.A.
 TU: Tulane University, New Orleans, LA, U.S.A. (material now at PRI)
 UCMP: University of California Museum of Paleontology, Berkeley, CA, U.S.A.

STRATIGRAPHIC DISTRIBUTION

Five species of neritid gastropods assigned to three genera occur in the Neogene sediments of the Yaque Group of the Cibao Valley: *Nerita fulgurans* Gmelin, 1791; *Neritina figulopicta* Maury, 1917; *Neritina dom-*

inicana, n. sp.; *Neritina jungi*, n. sp.; and *Smaragdia viridis* (Linnaeus, 1758). Approximately 111 NMB and six TU samples contain more than 1300 neritid specimens. These samples were collected from exposures along the Río Cana, Río Gurabo, Río Mao, and the Río Yaque del Norte (see Text-fig. 1). No samples containing identifiable neritids were collected in the Río Amina section, the Santiago section, the Arroyo Puñal section, or the Río Verde section (see Saunders *et al.*, 1986, text-fig. 3).

The overall stratigraphic distributions of neritid species from NMB samples are shown in Text-figure 2, and a summary of species abundances by river section is shown in Text-figure 3. *Nerita fulgurans* is rare (one



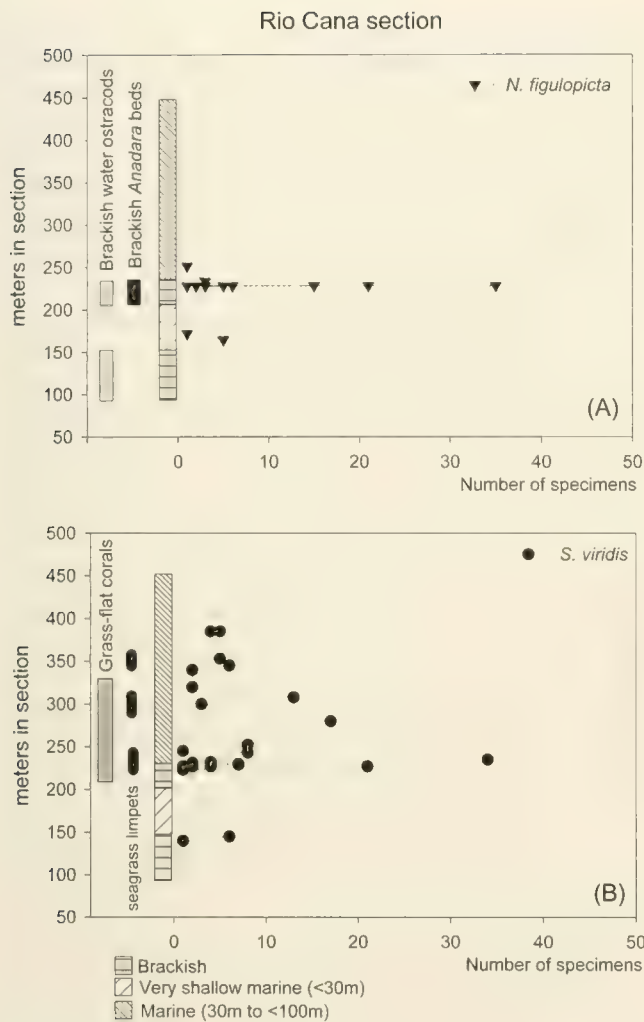
Text-figure 3.—Relative abundances of neritids in the Río Yaque del Norte (López), Río Mao, Río Gurabo, and Río Cana stratigraphic sections. See Text-figure 1 for the geographic locations of river sections.

specimen) and occurs in the Mao Formation of the Río Gurabo. *Neritina dominicana* is also rare (two specimens from one NMB sample) and is restricted to the Cercado Formation of the Río Cana section. *Neritina figulopicta* is abundant (more than 300 specimens from 35 NMB samples) and occurs in the Cercado and Gurabo formations of the Río Cana, the Cercado and Gurabo formations of the Río Gurabo, the Cercado and Gurabo formations of the Río Mao, and the Baitoa formation of the Río Yaque del Norte at López. *Smaragdia viridis* is the most abundant Dominican neritid (more than 700 specimens from 73 NMB samples) and occurs in the Cercado and Gurabo formations of the Río Cana, the Cercado and Gurabo formations of the Río Gurabo, the Cercado and Gurabo formations of the Río Mao, and the Baitoa Formation of the Río Yaque del Norte at López. *Neritina jungi* is rare (two specimens from two NMB samples) and occurs in the Cercado Formation of the Río Cana and the Gurabo Formation of the Río Gurabo.

Río Cana (see Text-fig. 4A–B).—45 NMB samples containing approximately 278 neritid specimens were collected from the Río Cana. These samples contain *Neritina dominicana*, *Neritina jungi*, *Neritina figulopicta* and *Smaragdia viridis*. *Smaragdia viridis* is the most abundant species in the section (172 specimens) and occurs in 27 NMB samples. It first appears at NMB 17026 at approximately 140 m in the Cercado Formation and last occurs at NMB 16833 at approximately 385 m in the Gurabo Formation. The abundance of *S. viridis* fluctuates through the section, but most samples and specimens occur between 230 m and 310 m in the section. Abundance peaks near 235 m. *Neritina figulopicta* is the second most abundant neritid in the Río Cana section (about 100 specimens) and occurs in 15 NMB samples. *Neritina figulopicta* is restricted to the Cercado Formation and first appears at NMB 16856 at approximately 165 m in the section and last appears at NMB 16835 at approximately 252 m in the section. Nearly all samples containing *N. figulopicta* are from 220 to 230 m in the section, and this species is most abundant near 228 m. *Neritina jungi* is rare (two specimens) and occurs in two NMB samples: NMB 16841 and NMB 16843 at approximately 228 m in the Cercado Formation. *Neritina dominicana* is also rare (two specimens) and occurs in NMB 16850 at approximately 228 m in the Cercado Formation (Text-fig. 4A–B).

Río Gurabo (see Text-fig. 5A–B).—34 NMB samples containing approximately 511 neritid specimens were collected from the Río Cana. These samples contain *Neritina fulgurans*, *Neritina jungi*, *Neritina figulopicta* and *Smaragdia viridis*. *Smaragdia viridis* is the most abundant species in the section (291 specimens) and occurs in 18 NMB samples. It first occurs at NMB 15916 at approximately 90 m in the Cercado Formation and last occurs at NMB 15849 at approximately 275 m in the Gurabo Formation. The abundance of *S. viridis* peaks near 120 m and again near 200 m in the section, but most samples and specimens occur between 75 m and 130 m. *Neritina figulopicta* is the second most abundant neritid in the Río Gurabo section (219 specimens) and occurs in 13 NMB samples. *Neritina figulopicta* first appears at NMB 16213 at approximately 40 m in the Cercado Formation and last appears at NMB 15906 at approximately 130 m in the Gurabo Formation. The abundance of *N. figulopicta* peaks near 56 m in the Gurabo section. *Neritina jungi* is rare (one specimen) and occurs in TU 1378 in the Gurabo Formation (see Text-fig. 5A–B).

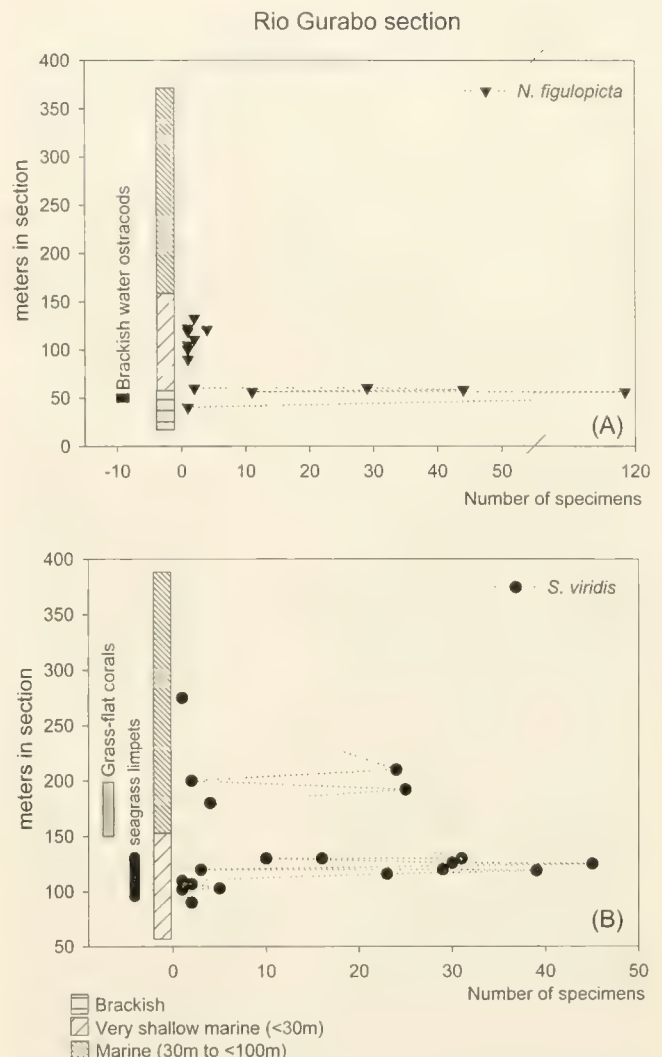
Río Mao.—The 20 NMB samples containing neritids are restricted to three sampling areas: Maury's Bluff One, Two, and Three (see Maury, 1917; Saunders *et al.*, 1986). Faunal and microfossil evidence



Text-figure 4.—Stratigraphic distributions of NMB samples containing Neritid species, and the number of specimens in each sample, in the Río Cana section. (A). *N. figulopicta*. (B). *S. viridis*. Samples represent a collection of specimens from a stratigraphically defined position (see the APPENDIX and Saunders *et al.*, 1986, pp. 41–64).

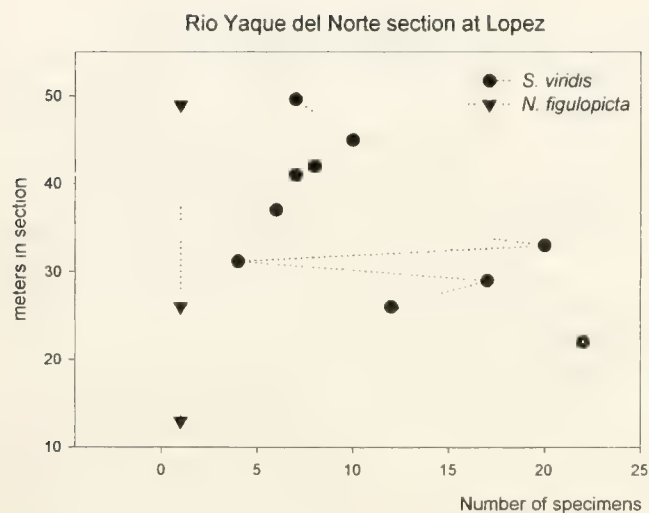
suggests that the Río Mao bluffs should be assigned to the upper Cercado or lower Gurabo Formations (Saunders *et al.*, 1986). Samples from the Río Mao section contain *Neritina figulopicta* and *Smaragdia viridis*. The latter is very abundant and occurs in 17 NMB samples. It is most abundant in TU 1294 (279 specimens). In contrast, *N. figulopicta* is rare (three specimens) and occurs in three NMB samples.

Río Yaque del Norte (see Text-fig. 6).—The López samples from the Baitoa Formation contain the oldest neritids from the Cibao Valley. The data presented here include the stratigraphic positions of NMB samples above Horizon A, a discordant erosive contact below poorly sorted conglomerates (see Saunders *et al.*,



Text-figure 5.—Stratigraphic distributions of NMB samples of *N. figulopicta* and *S. viridis*, and the number of specimens in each sample, from the Río Gurabo section. (A). *N. figulopicta*. (B). *S. viridis*. Samples represent a collection of specimens from a stratigraphically defined position (see the APPENDIX and Saunders *et al.*, 1986, pp. 41–64).

1986). Both *Neritina figulopicta* and *Smaragdia viridis* occur in the Baitoa Formation. *Smaragdia viridis* is abundant (113 specimens) and occurs in 10 NMB samples. It first appears in NMB 17286 at approximately 22 m in the section and last appears in NMB 16942 at approximately 50 m in the section. *Smaragdia viridis* is most abundant from 20 m to 35 m in the section. *Neritina figulopicta* is rare (three specimens) and occurs in three NMB samples. It first occurs in NMB 17283 from approximately 13 m in the section and last occurs at NMB 17287 from approximately 49 m in the section.



Text-figure 6.—Stratigraphic distributions of NMB samples containing *N. figulopicta* and *S. viridis*, and the number of specimens in each sample, from the Río Yaque del Norte section at López. Samples represent a collection of specimens from a stratigraphically defined position (see the APPENDIX and Saunders, Jung, and Bijou Duval (1986, pp. 41–64).

PALEOECOLOGY

Neritid genera have restricted environmental and ecological associations and therefore have great potential as paleoenvironmental and paleoecological indicators in the fossil record. Specifically, the presence, abundance, and distribution of *Smaragdia* species, which are obligatory seagrass epibionts, provide strong evidence for the presence and distribution of seagrasses in the Neogene of the Cibao Valley, even though no seagrasses are preserved in these sections. In addition, the presence, abundance, and distribution of *Neritina* species, which are frequently restricted to freshwater and/or brackish-water habitats, provide evidence for the presence and distribution of brackish paleoenvironments. In this study the stratigraphic ranges of neritid species are compared to previous bathymetric and paleoecological reconstructions using ostracods (Bold, 1988), corals (Saunders *et al.*, 1982, 1986; Budd *et al.*, 1996), and mollusks (Saunders *et al.*, 1982, 1986; Anderson, 1996). In addition, the stratigraphic ranges and abundances of *Smaragdia viridis* in the Cana and Gurabo sections are compared to the distribution of previously hypothesized seagrass beds.

Río Cana.—The Río Cana section contains brackish, shallow marine, and deep marine sediments deposited in progressively offshore and more open marine conditions upsection. Brackish-water ostracods occur below 150 m in the section and between 200 m and 230 m in the middle Cercado Formation (Bold, 1988). The

brackish water *Larkinia-Mytilus-Melongena* mollusk assemblage also occurs in the middle Cercado Formation (Saunders *et al.*, 1982) as do several brackish water *Anadara patricia* and oyster beds. Sediments of shallow marine origin (<30 m depth) occur from 150 m to 200 m in the section, whereas sediments of slightly deeper marine origin (>30 m depth) occur from 230 to 450 m in the section (Saunders *et al.*, 1986; Bold, 1988; Anderson, 1996).

Neritina figulopicta first occurs near 160 m in the section, but most samples and specimens occur from 200 to 230 m; these sediments are considered to be of brackish-water origin (Bold, 1988). *Smaragdia viridis* first appears near 140 m in the section in sediments of brackish water origin. Abundance is very low until 230 m in the section, just above the brackish water interval containing most samples of *N. figulopicta* (Saunders *et al.*, 1986; Bold, 1988). The interval of abundant *S. viridis* coincides with the presence of grass-flat coral assemblages (Budd *et al.*, 1996) and seagrass-associated limpets (*e.g.*, *Patelloida*, D. R. Lindberg, personal communication 1998). The stratigraphic ranges of *S. viridis* and seagrass-associated limpets are much greater than the stratigraphic range of grass-flat coral assemblages (Text-fig. 4). Grass-flat coral assemblages last occur near 335 m in the section; *S. viridis* last occurs near 400 m in the section; and seagrass-associated limpets last occur near 360 m in the section. *Prunum maoense*, a seagrass-associated marginellid gastropod (Nehm, 2001), last occurs in the Río Cana section near 340 m and coincides with the last occurrence of grass-flat coral assemblages. The stratigraphic overlap of grass-flat coral assemblages, seagrass associated limpets, seagrass associated marginellids, and *S. viridis* from 230 to 320 m in the Río Cana section strongly suggests the presence of seagrasses in this stratigraphic interval.

Río Gurabo.—The Río Gurabo section contains brackish, very shallow marine, shallow marine, and deep marine sediments deposited in progressively offshore and more open marine conditions upsection. The Cercado Formation contains brackish and very shallow marine deposits. The brackish water *Larkinia-Mytilus-Melongena* mollusk assemblage, which occurs in the Cercado Formation of the Río Cana, also occurs in the lower Cercado Formation of the Río Gurabo from approximately 20 to 50 m. Brackish water ostracod species also occur near 50 m in the middle Cercado Formation (Saunders *et al.*, 1986; Bold, 1988).

As in the Río Cana section, *Neritina figulopicta* occurs most abundantly in sediments hypothesized to be of brackish-water origin (Saunders *et al.*, 1982, 1986; Bold, 1988). *Neritina figulopicta* first occurs near 40 m in the section, and then increases in abundance from

50 to 60 m in the section (Text-fig. 5). *Neritina figulopicta* is uncommon (usually 1 to 3 specimens per sample) from 80 to 130 m in the section.

Smaragdia viridis first occurs in sediments of very shallow marine origin (>30 m depth) near 90 m in the section. Abundance increases substantially from 100 to 130 m in the section. This interval of abundant *S. viridis* is concordant with the distribution of seagrass-associated limpets (Text-fig. 5). Near 150 m in the section sediments are of a deeper marine origin (30 to 100 m depth). Grass-flat coral communities occur from approximately 150 to 190 m in the section (Budd *et al.*, 1996). *Smaragdia viridis* is also abundant in a few samples collected from 175 to 210 m in the Río Cana section.

As in the Río Cana section, *Neritina figulopicta* is most abundant in sediments hypothesized to be of brackish-water origin, and *Smaragdia viridis* is most abundant in sediments that also contain seagrass-associated limpets. Unlike in the Río Cana section, the stratigraphic distributions of seagrass-associated limpets are discordant with the distribution of grass-flat corals in the Río Gurabo section (Text-fig. 5). The interval of greatest abundance of *S. viridis* is also discordant with the distribution of grass-flat corals in the Río Gurabo section.

Río Yaque del Norte at López.—Unlike in the Río Cana and Río Gurabo sections, no clear faunal distribution patterns are apparent in the López section. Pebbly, well-bedded silts with conglomeratic and coarse sandy layers occur at López. The Baitoa Formation probably contains deposits from a much higher energy environment than that of the Cercado and Gurabo formations of the Río Gurabo and Río Cana (Saunders *et al.*, 1986). Using muricid gastropod ecological data, Vokes (1986) estimated the Baitoa Formation to be of shallow marine origin (0–20 m paleodepth). Ostracod data also suggest a shallow water paleoenvironment (Bold, 1988). Additionally, the absence of planktonic foraminifera and calcareous nannofossils in the first 20 m of the section also suggests very shallow marine paleoenvironments (Saunders *et al.*, 1982). The remaining 34 m of the section is more finely grained and contains frequent horizons with pebbles and cobbles. The presence of soritid foraminifera suggests the presence of *Thalassia* in the Baitoa Formation (Saunders *et al.*, 1986, p. 29). *Smaragdia viridis* occurs from about 20 m to 50 m in the section, and is most abundant from about 20 to 35 m. No information on seagrass-associated limpets or grass-flat coral assemblages is available for the Baitoa Formation, but the abundance and broad distribution of *S. viridis* and the rarity of *Neritina figulopicta* (three specimens) suggest that

the López section contained shallow marine seagrass beds and normal marine conditions.

SYSTEMATIC PALEONTOLOGY

Introduction

The five species of neritopsine gastropods treated herein are assigned to three genera in two subfamilies of the Neritidae. The Order Neritopsina encompasses six families with living representatives and a number of extinct families and genera (Knight *et al.*, 1960) that cannot be assigned to the order with a high level of confidence. The living taxa occur in terrestrial, freshwater, brackish, and fully marine habitats, with major habitat transitions having occurred a number of times in the evolutionary history of the group. The Neritidae is the only gastropod family that has evolved to occupy the full range of habitats. It is also the family with the best known, although not the longest fossil record, with representatives first appearing in the Triassic (Bandel, 1992, 1994). Only the Neritopsidae has a longer record, dating from the Devonian. The terrestrial Hydrocenidae and shell-less marine Titiscaniidae have no appreciable fossil record, and the terrestrial Helicinidae and marine Phenacolepadidae have a fragmentary record in the Cenozoic (Knight *et al.*, 1960). Solem (1979) and Solem and Yochelson (1979) recognized Late Paleozoic (Pennsylvanian) terrestrial helicinids. Bandel (1992) recognized only marine lineages in the Paleozoic, but his inclusion of the extinct Platyceratidae extends the record back into the Ordovician.

In an effort to clarify the relationships and evolutionary history of neritopsine gastropods, contemporary systematic studies of the family have placed increasing emphasis on soft anatomical features (e.g., Holthuis, 1995; Sasaki, 1998) and radular morphology (e.g., Unabia, 1996). However, the shell is rich in features that are adequate for recognition of species and higher taxa, and shell features must provide the ultimate key to explaining the fossil record. Classification of the group is sufficiently unstable at present that we have chosen to allocate the Dominican fossil species to traditional supraspecific taxa. Most of these taxa have distinctive shell characters, and so we have provided diagnoses for higher categories as well as species. Diagnoses include only those features necessary and sufficient to distinguish the taxon from other taxa. Descriptions are given for species only and include a full account of the morphology, including features that may be shared with other taxa. In the case of *Neritina figulopicta* and *Smaragdia viridis*, the description is an expansion of the original description, based on large samples of new fossil material.

Prior to this paper, only the two most abundant species, *Neritina figulopicta* and *Smaragdia viridis* (as *N. viridemar*), had been reported from the Neogene of the Dominican Republic (Maury, 1917). Of the remaining three species, *Nerita fulgurans* is a living species recorded here for the first time from the fossil record, and the remaining two species, *Neritina dominicana* and *Neritina jungi*, are new.

Color Pattern Polymorphism and Systematics

Color polymorphism occurs in gastropods from marine, freshwater, and terrestrial habitats. It has been studied most thoroughly in marine arboreal (mangrove) littorinids (Hughes and Jones, 1985; Hughes and Mather, 1986; Ekendahl and Johannesson, 1997; Ekendahl, 1998) and the terrestrial pulmonate *Cepaea nemoralis* (Cain and Sheppard, 1950). In both of these systems, the color morphs are discrete and genetically determined, and variation in color morph frequencies among habitats is attributed to natural selection for crypsis in the presence of visual predators and other factors (Ekendahl and Johannesson, 1997).

In fully marine gastropods, discrete color polymorphism is uncommon. Phenotypic variation in coloration has been shown experimentally to be influenced by diet in many primitive marine gastropods, including haliotids (Leighton, 1961), turbinids (Ino, 1958), and trochids (Creese and Underwood, 1976; Underwood and Creese, 1976). In these taxa the differences in pattern morph frequencies between populations do not require genetic differences between morphs and are not a consequence of natural selection (Underwood and Creese, 1976).

In some marine gastropods, color patterns are unique at the level of the individual, and there is intergradation among pattern types. When extreme color pattern polymorphism occurs in infaunal gastropods, as in the trochid genera *Umbonium* and *Bankivia* (Hickman and McLean, 1990), there is little basis for postulating an adaptive function. Extreme color polymorphism may be more typical of traits that are shielded from natural selection and may be epiphenomenologically linked to the pattern of mantle edge activity that secretes the shell.

Shell pigments and color patterns are nowhere more varied and complex than in the gastropod family Neritidae. Most authors have not attempted to discover order in this variation. In the original description of *Smaragdia chipolana*, Dall (1892) referred to lines of pigment "in every conceivable form of zigzag or curve." Gardner (1947) described the pattern on this same species as "curiously sketchy and oriental in design." Vokes (1990) concurring with Gardner on "the beauty of these tiny works of art, which do look much

as if they were decorated by an oriental calligrapher," captured the variation visually in a series of 24 illustrations without attempting to classify patterns.

Early attempts to bring order to the phenomenon of molluscan shell pigmentation focused on classifying the remarkable array of pattern elements (e.g., axial lines, spiral bands, squares, polygons, checkerboards, reticulate networks, elaborate zig-zags, discrete spots, irregular blotches), the arrangement and configuration of elements, and the combinations and periodicity of elements (Oberling, 1968). Because many patterns show intergradation, discrete classifications are difficult. Grüneberg (1982) referred to the pattern of pigmentation in the neritid *Clithon oualanensis* (Lesson, 1831) as a "pseudopolymorphism," although we see no need for a separate designation for extreme variation, particularly in the absence of demonstrably continuous variation. The most detailed attempt to classify color patterns and analyze pattern variation in a neritid is that of Neumann (1959) for *Theodoxus fluviatilis* Linnaeus, 1758. Safriel (1969) noted continuous variation in color pattern in the shells of two neritid species at Elat, but classified them into only three categories based on the predominance of black, red, or white pigment.

In spite of their apparent complexity, molluscan pigment patterns can be simulated with relatively few model equations (e.g., Waddington and Cowe, 1969; Cowe, 1971; Lindsay, 1982; Meinhardt and Klingler, 1987). Different patterning models can, in fact, produce identical results, making it difficult to assess the relationship between model instructions and the actual biological mechanism by which patterns are generated. Ermentrout *et al.* (1986) developed a neural model of the organization of pigment secretion to explain the variety of patterns produced by the fresh-water *Neritina turrita* Chemnitz, 1786. In designating pattern classes, we have emphasized consistency of recognition. The classes bear no relationship to how they were generated.

Pigments and color patterns are rarely preserved in the fossil record. There are, however, reports from the Lower Paleozoic onward. Most accounts are of single remarkable individuals or a hand full of specimens. Patterns of variation in larger populations have, however, been documented in Paleozoic pleurotomariids (Hoare and Sturgeon, 1978) and platycerids (Kríz and Lukes, 1974; Yochelson and Kríz, 1974).

It is not uncommon to find patterns exquisitely preserved on fossil neritids when no trace of color is preserved on any other taxa in the same sample. The outstanding preservation of color patterns in large samples of *S. viridis* and *N. figulopicta* from multiple horizons and stratigraphic sections in the Cibao Valley

of the Dominican Republic provides a rare opportunity to examine the phenomenon of complex color polymorphism on a macroevolutionary temporal scale. In addition, the well-studied geological framework of the Dominican Republic permits comparisons of color polymorphism relative to sedimentological and associated faunal evidence.

SYSTEMATICS

Class **GASTROPODA**

Subclass **ORTHOGASTROPODA** Ponder and Lindberg, 1995

Order **NERITOPSINA** Cox and Knight 1960

Superfamily **NERITOIDEA** Rafinesque, 1815

Family **NERITIDAE** Rafinesque, 1815

Diagnosis.—Inner shell walls resorbed in adults so that interior forms single cavity. Columellar lip calcified, forming prominent shelf or deck with straight margin. Operculum calcified, semicircular, fitting tightly in aperture and articulating against edge of deck.

Remarks.—The family includes taxa that secondarily have lost (through size reduction and internalization) a functional operculum (Vermeij, 1969) and assumed a nearly planispiral coiling and limpet-like form. Most neritid species are classified either under one of the subgenera of the marine genus *Nerita* Linnaeus, 1758, or one of the subgenera of the brackish to freshwater genera *Septaria* Férussac, 1807, and *Neritina* Lamarck, 1816. Neritids first appear in marine rocks of Triassic age (Knight *et al.*, 1960; Bandel, 1992, 1994).

Subfamily **NERITINAE** Rafinesque, 1815

Diagnosis.—As presently constituted, this taxon cannot be diagnosed.

Remarks.—In all of the existing subfamily classifications except that of Holthuis (1995), Neritinae is an unnatural grouping of taxa that lack any defining synapomorphies of the shell, radula, or anatomy. Holthuis restricted the Neritinae to the genus *Nerita*, placing all the remaining neritid genera and subgenera under the Theodoxinae. This arrangement is equally problematic for the paleobiologist because the defining synapomorphies of the Theodoxinae are all from soft tissues. We have elected to retain a subfamily classification both for the sake of stability until revisionary systematics are completed and because Smaragdiinae, as discussed below, is a significant clade ecologically as well as morphologically within the Neritidae.

Genus **NERITA** Linnaeus, 1758

Dontostoma Klein, 1753, p. 16.

Dontostoma "Klein" Hermannsen, 1847, p. 404.

Dontostoma "Klein" Adams and Adams, 1858, p. 656.

Neritarius Duméril, 1806, p. 164.

Tenare Gray, 1858, p. 93.

Type species.—*Nerita peloronta* Linnaeus, 1758; by subsequent designation, Montfort, 1810, p. 347. Recent: Florida, West Indies, Bermuda.

Diagnosis.—Shell relatively large (frequently >2 cm wide), anomphalous, thick, and globular or turbanate in outline, with porcellanous surface and relatively inflated final whorl. Columellar deck flat, with few prominent marginal denticles and surface ranging from smooth to pustulose, lirate, or irregularly wrinkled. Outer lip of shell thick, with two or more denticles. Operculum with extension (=peg or apophysis) projecting into dorsal surface of foot and with extra calcareous layer on top of corneous layer on exterior surface.

Remarks.—Eldredge (1987) listed approximately 500 nominal living species described under *Nerita*, although Holthuis (1995) suggests that there are probably no more than 65 species in the genus as it is currently constituted and after synonyms and unavailable names have been eliminated. *Nerita* species are almost exclusively tropical and subtropical and occur predominantly in intertidal and supratidal habitats, where they are physiologically capable of withstanding exposure to air and high temperatures for sustained periods.

Shell distinctions between the neritid subgenera are by no means clear, and subgeneric distinction is not employed here, although the Dominican species is similar in many features to the type species of the genus, and therefore to *Nerita s.s.* The earliest fossils of *Nerita s.s.* are from the Paleocene of the West Indies.

Nerita fulgurans Gmelin, 1791

Text-fig. 7

Nerita fulgurans Gmelin, 1791, p. 3685.

Nerita antillarum Gmelin, 1791, p. 3685.

Nerita lindae Petuch, 1988, p. 151, pl. 30, figs. 4, 5, 11.

Diagnosis.—Inner edge of outer lip with 16 large teeth. Two posterior teeth wider than others and protruding into aperture. Three anterior teeth of medium size. Edge of columellar lip bearing two sets of teeth: central set composed of two large rounded teeth extending over parietal area that are as wide as interspaces; posterior set composed of single, very large quadrate tooth. Spiral cords bifurcate towards outer lip.

Description.—Shell large, reaching 22.0 mm in height by 25.9 mm in width, with 3 whorls; globose, thick, opaque; surface bearing 27 flat-topped spiral cords, which are wider than interspaces, bifurcate towards outer lip, and axially marked by submicroscopic growth lines. Protoconch eroded away in all material examined. Spire low, suture inconspicuously im-



Text-figure 7.—*Nerita fulgurans* Gmelin, 1791, NMB locality 15833, Río Gurabo Section. Ventral side, shell height 21.1 mm. NMB H 18230.

pressed, shoulder and body whorl rounded in cross section. Aperture lunate; outer lip thick with sharp margin. Margin inner edge with 16 large teeth, two posterior teeth wider than others and protruding, three anterior teeth of medium size; parietal callus thick, flat to concave, with papillose anterior half, and six folds near abapertural rim of its posterior half. Columellar lip slightly concave, its edge bearing two sets of teeth: central set composed of two large rounded teeth extending over parietal area. Central teeth as wide as interspaces; posterior set composed of single, very large, quadrate tooth; anterior third of columellar lip edge toothless.

Ground color white in Recent specimens, yellowish in fossil specimens, overlain by obscure black mottling in Recent shells, dark green in fossil specimens. Aperture color white to yellow.

Type material.—Gmelin (1791), in his description of *Nerita fulgurans*, did not refer to any specimen in a collection. Thus, a Recent specimen, UCMP No. 39943, from UCMP locality S-4, measuring 26.0 mm in height by 29.1 mm in width, is herein designated as the Neotype of *N. fulgurans*.

Type locality.—Cartagena Bay, Colombia, site where the Neotype was collected, is here designated as the type locality, as the original locality “*ad Insulas Americae*” (Gmelin, 1791) is too vague to be associated with the presently known distribution of *Nerita fulgurans*.

Material.—One specimen deposited in the collection of Natural History Museum, Basel: NMB locality 15833. Recent specimens are in the collections of Mu-

seu Oceanográfico Prof. E. C. Rios Fundação Universidade do Rio Grande (MORG), and Col. Mol. F.H.A. Costa (FHAC).

Remarks and comparisons.—The occurrence of *Nerita fulgurans bernhardi* (Récluz, 1855) in the west coast of North America, from the Gulf of California to Panamá (Tryon, 1888), has yet to be confirmed, as we know of no specimen of *N. fulgurans* s.s. that was collected in the Eastern Pacific. Moreover, Keen (1971) and Abbott (1974) considered *N. bernhardi* as a junior synonym of *Nerita funiculata* Menke, 1851, the latter occurring from Baja California to Peru, and the Galápagos Islands.

Jung (1965) studied neritid fossils from Miocene and Pliocene deposits of Venezuela, which he assigned to *Nerita fulgurans*, despite the differences from Recent specimens that he pointed out. After studying Miocene samples from Trinidad, Jung (1969) considered this material to be conspecific with the Venezuelan fossils that he had previously assigned to *N. fulgurans* and identified the fossils from both localities as *Nerita exuvioides* Trechmann, 1935. The taxonomic status of *N. exuvioides*, a species from lower middle Miocene to lower Pliocene of Panamá and Cariacou, was clarified by Vokes (1983). Later on, the fossils from Venezuela and Trinidad studied by Jung (1965, 1969) were noted to belong neither to *N. fulgurans* nor to *N. exuvioides*, but instead to *Nerita fortidentata* Vermeij and Collins, 1988, when the latter species was described from the Upper Miocene to the Lower Pliocene deposits of Panamá (Vermeij and Collins 1988). Hence, true fossils of *N. fulgurans* were unknown until the present study, for Russell (1941), Vokes (1983), and Vermeij and Collins (1988) had considered *N. fulgurans* to be a constituent of the Recent tropical Western Atlantic fauna.

Petuch (1988) described *Nerita lindae* from the Recent rock reefs of Florida and considered this species to be the closest relative of *N. fulgurans*. *Nerita lindae*, however, cannot be distinguished from juvenile specimens of *N. fulgurans* from Colombia and Venezuela.

Nerita fulgurans is considered the closest relative of *Nerita fortidentata* from the Upper Miocene to the Lower Pliocene of Panamá (Vermeij and Collins, 1988); the latter can readily be separated from the former by its strong central columellar teeth, its posterior parietal fold which curves into the aperture, its 10 strong folds on the parietal callus (6 occur in *N. fulgurans*), and its 12 teeth on the inner edge of the outer lip (16 occur in *N. fulgurans*). Moreover, the bifurcate spiral cords of *N. fulgurans* do not occur in *N. fortidentata*.

Occurrence.—NMB locality 15833, Río Gurabo Section, Mao Formation.

Distribution.—Pliocene: northern Dominican Republic. Recent: Bermuda, southeast Florida, Gulf of Mexico, Colombia, Venezuela, Cuba, Puerto Rico, Curacao, Maranhao and Bahia in northeast Brazil.

Genus **NERITINA** Lamarck, 1816

Neritella Humphrey, 1797, p. 57.

Neritella "Humphrey" Gray, 1847, p. 148.

Labialia "Megerle" Scudder, 1882, p. 177.

Onchina "Megerle" Scudder, 1882, p. 234.

Type species.—*Nerita pulligera* Linnaeus, 1766; subsequent designation Children, 1823 (ICZN Opinion 119, 1931). East Indies, Australia, Central Polynesia.

Diagnosis.—Shell small (typically <2 cm wide), anomphalous, thin, with sharp outer lip. Columellar deck smooth. Columellar lip smooth or with multiple fine or weak marginal denticles.

Remarks.—Species of *Neritina* are distinguishable from those of *Nerita* by their smaller and thinner shells and thin outer lip. The shell surface is typically smooth and unsculptured, and complex color patterns are common. Like *Nerita*, the genus is cosmopolitan and predominantly tropical and subtropical. *Neritina* species occur in freshwater, estuaries, and other habitats with freshwater input and less than full-marine salinities

Genus **NERITINA** Lamarck, 1816

Neritina figulopicta Maury, 1917

Text-fig. 8

Neritina (*Puperita*) *figulopicta* Maury, 1917, p. 152, pl. 24, fig. 10.

Diagnosis.—Parietal callus projecting into aperture and reducing its area. Free edge of columella bearing three sets of teeth with one large, rhomboid, intermediate tooth between every two sets of teeth. Anterior set of teeth composed of one to two medium and rounded teeth, wider than interspaces; median set of teeth composed of three small and sharp teeth narrower than interspaces; posterior set of teeth composed of two to three inconspicuous rounded teeth.

Description.—Shell small, reaching 14.9 mm in height by 16.2 mm in width; globose to ovate, thick, opaque; surface smooth with microscopic growth lines. Teleoconch with 3.5 whorls. Protoconch papiliiform, paucispiral, with surface eroded in all the specimens studied. Spire low to slightly elevated, suture impressed, shoulder rounded, body whorl rounded in cross section. Aperture lunate, small; outer lip thin, smooth inside, bulging on its anterior half; parietal callus convex, thick, smooth, steadily expanding towards anterior end, projecting towards, and constricting size of aperture; exhalant groove deeply impressed, long, narrow, and transversely oriented. Collumellar lip straight to slightly concave, its free edge bearing three

sets of teeth with one large, rhomboid, intermediate tooth between every two sets of teeth. Anterior set composed of one to two medium, rounded teeth, wider than interspaces; median set composed of three small and sharp teeth, narrower than interspaces; posterior set composed of two to three inconspicuous rounded teeth. Ground color white overlain by black line patterns (color morphs) divided into the following groups (see Text-fig. 9):

Interrupted (I). Zigzag axial lines are interrupted on three spiral sections: one at the shoulder, one at the midbody, and one at the base of the shell. Approximately 4% of the specimens we studied are of pattern I;

Zigzag (Z). Zigzag, continuous, axial lines extend from the suture to the base. Approximately 20% of the specimens we studied are of pattern Z;

Textile (T). Parallel, axial lines are interrupted in some sections and branch inwards from two to six lines in the other sections. Approximately 36% of the specimens we studied are of pattern T;

Banded (B). Branched axial lines are arranged in two spiral bands, one from suture to shoulder, and the other at the mid-body. Approximately 9% of the specimens we studied are of pattern B;

Diagonal (D). Diagonal lines extend from either the suture or the shoulder to the base of the shell. Short and wavy axial lines run perpendicular to the diagonal line on the adapical side. These lines resemble a comb-like structure. Approximately 4% of the specimens we studied are of pattern D;

Network (N). Parallel, wavy, and thin axial lines are interrupted by open spaces, and a thick line marginates the adapertural side of each open space. Approximately 26% of the specimens we studied are of pattern N;

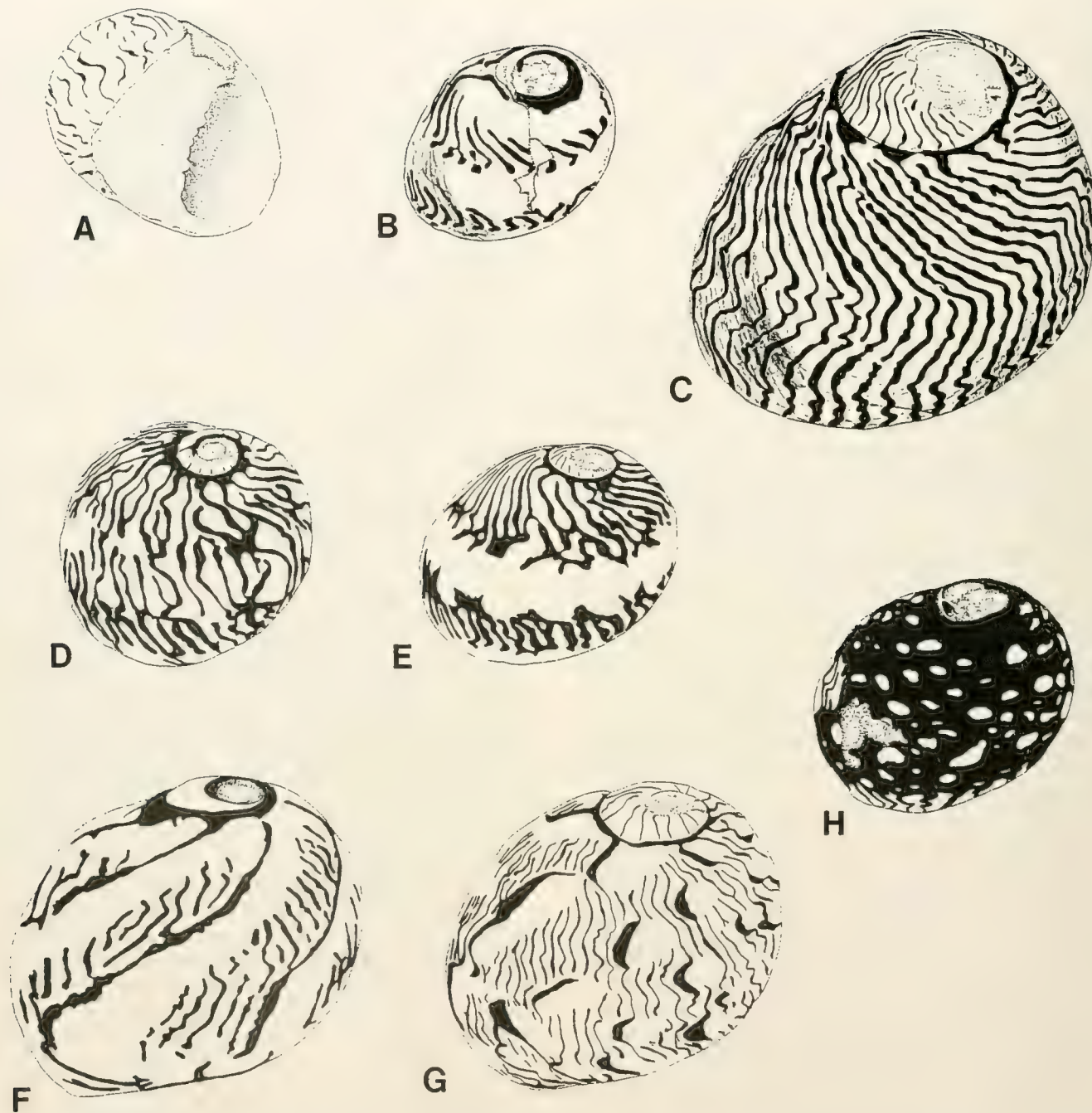
Spotted (S). Closely arranged submicroscopic axial lines cover almost the whole shell, and elliptical uncolored spots are unevenly spaced among the axial lines. Approximately 1% of the specimens we studied are of pattern S.

Type material.—In the original description of *Neritina figulopicta*, Maury (1917) did not list a type specimen. PRI houses the holotype (PRI 28849).

Type locality.—"Gravels of the Río Cana near Caimito" (Maury 1917), in the northern Dominican Republic.

Material.—A total of 327 specimens are deposited in the collections of NMB, and the University of California Museum of Paleontology, Berkeley.

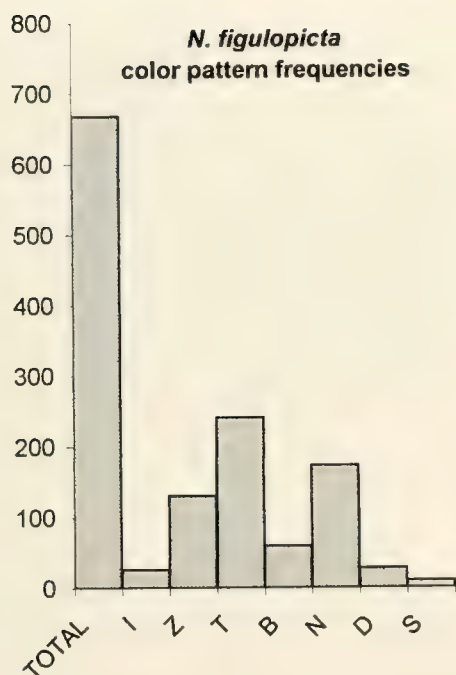
Remarks and comparisons.—*Neritina figulopicta* was originally placed in the subgenus *Puperita* Gray, 1857, and also considered to be the ancestor of the living West Indian *Puperita pupa* (Linnaeus, 1758) by Maury (1917). We believe that Maury (1917) estab-



Text-figure 8.—*Neritina figulopicta* Maury, 1917. a: NMB locality 15920, Río Gurabo Section, ventral side, shell height 2.9 mm; b: NMB locality 15919, Río Gurabo Section, dorsal side, pattern I (interrupted), shell height 2.7 mm; c: NMB locality 15919, Río Gurabo Section, dorsal side, pattern Z (zigzag), shell height 6.5 mm; d: NMB locality 15919, Río Gurabo Section, dorsal side, pattern T (textile), shell height 3.0 mm; e: NBM locality 16843, Río Cana Section, dorsal side, pattern B (banded), shell height 3.2 mm; f: NMB locality 15919, Río Gurabo Section, dorsal side, pattern D (diagonal), shell height 4.8 mm; g: NMB locality 15919, Río Gurabo Section, dorsal side, pattern N (network), shell height 4.6 mm; h: NMB locality 16846, Río Cana Section; dorsal side, pattern S (spotted), shell height 3.2 mm.

lished a relationship between these two species based on the fact that fossils of *N. figulopicta* exhibit a white ground color with black, axial, zigzag, and bifurcate black stripes similar to those of *P. pupa*. However, the

latter species is not as phenotypically variable as the former. Moreover, shells of the genus *Puperita* are known for having obscure spiral ribs, a narrow columellar area, a columellar edge with small denticles in



Text-figure 9.—Color pattern morph frequencies for *Neritina figulopicta* Maury, 1917. See text and Text-figure 8 for color morph descriptions.

the middle, and a relatively large posterior tooth (Komatsumi, 1986). In contrast, *N. figulopicta* lacks these characters. Thus, based on shell characters, *N. figulopicta* is herein removed from *Puperita*.

Neritina virginea (Linnaeus, 1758) of the Recent western Atlantic, is considered herein to be a close relative of *Neritina figulopicta*. The color pattern of the shells alone does not allow for a distinction between these two species. Moreover, the dentition pattern of the columellar edge follows the same pattern in both species. In contrast, there are submicroscopic differences in tooth morphology between the two species: the two large, intermediate teeth, and the teeth of the median set, are bifurcated in *N. virginea*, whereas in *N. figulopicta* those teeth are simple. Finally, the posterior set of teeth is composed of five to seven plicae in *N. virginea* but in *N. figulopicta* the set is composed of only two to three short and rounded teeth.

Occurrence.—(see APPENDIX): Río Cana Section: NMB localities 16835, 16838, 16841, 16842, 16843, 16844, 16846, 16848, 16850, 16851, 16855, 16856, 16872, 16988, 17003.

Río Gurabo Section: TU 1358, 1378, NMB localities 15900, 15903, 15906, 15910, 15911, 15912, 15915, 15916, 15918, 15919, 15920, 16204, 16213.

Río Mao section: NMB localities 16917, 16923, 16926.

Río Yaque del Norte Section: NMB localities 17283, 17278, 17287, 17288

Distribution.—*Neritina figulopicta* occurs in Miocene and Pliocene deposits of the northern Dominican Republic. Neither fossils nor living specimens have yet been reported outside the Dominican Republic.

Neritina dominicana, new species

Text-fig. 10

Diagnosis.—Shell bulged immediately below shoulder area resulting in a subtriangular outline when shell is viewed from dorsal or ventral side; sutural ramps conspicuously concave; free edge of columellar lip bearing seven rounded and large teeth that are wider than interspaces and relatively uniform in size; third tooth (from the anterior end) is slightly wider than other teeth.

Description.—Shell small, reaching 3.2 mm in height by 3.1 mm in width, globose and bulged immediately below shoulder area thereby conferring a subtriangular outline to shell when viewed from either dorsal or ventral side. Shell thick, opaque, surface smooth and shiny with microscopic growth lines. Teleoconch with 2.3 whorls. Protoconch papilliform, paucispiral, with eroded surface. Spire low, suture deeply impressed, sutural ramps conspicuously concave, shoulder and body whorl rounded in cross section. Aperture lunate, wide; outer lip thick, smooth inside, bulging below shoulder area; parietal callus flat, thin, smooth, expanded on both posterior and anterior thirds, and with an excavated area near base; exhalant groove impressed, long, narrow, and transversely oriented. Columellar lip straight, with free edge bearing seven rounded and large teeth, wider than interspaces, and relatively uniform in size; third tooth from anterior end slightly wider than other teeth.

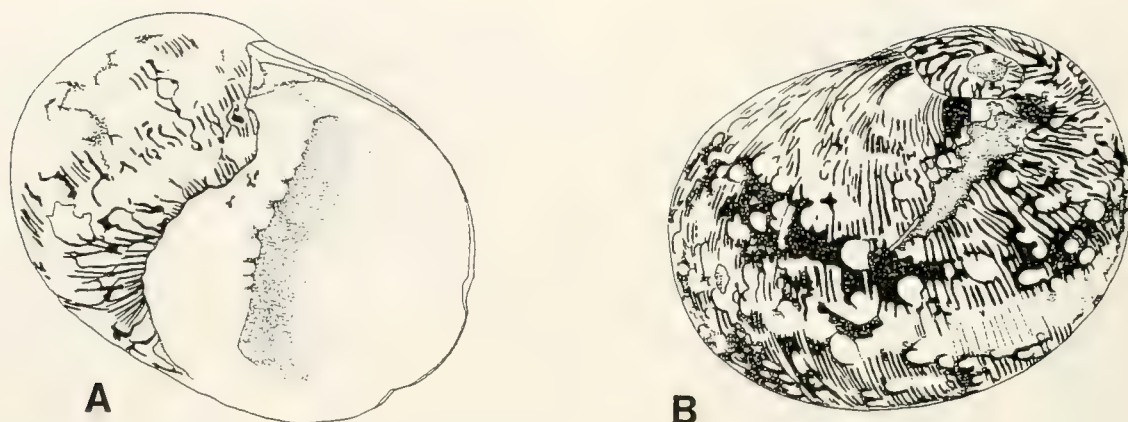
Ground color beige overlain with brown, wavy, broken axial lines, which are somewhat thicker and interconnected in three spiral bands: one at shoulder, one below midbody, and one at base of shell.

Type material.—Holotype NMB H 18231, measuring 3.0 mm in height by 2.9 mm in width. Paratype NMB H 18232 measuring 3.2 mm in height by 3.1 mm in width.

Type locality.—NMB locality 16850, Río Cana Section, Cercado Formation, northern Dominican Republic.

Material.—*Neritina dominicana* is presently known only from the two specimens from NMB locality 16850.

Remarks and comparisons.—No other fossils of the genus *Neritina* resemble *N. dominicana*. The shell characters of *N. dominicana* indicate some degree of similarity with low spired, young forms of *Neritina*



Text-figure 10.—*Neritina dominicana*, new species, NMB H 18231 (Holotype), NMB locality 16850, Río Cana Section. a: ventral side; b: dorsal side; shell height 3.0 mm.

virginea (Linnaeus, 1758), a constituent of the Recent western Atlantic fauna. The convex parietal area, concave columellar lip, three sets of small to medium columellar teeth with one large tooth between each set, the lack of conspicuous concavity on sutural ramps, and an outer lip expanded on its anterior half in *N. virginea* however readily set it apart from its fossil congener. Another constituent of the Recent Caribbean fauna, *Neritina punctulata* Lamarck, 1816 is somewhat similar to *N. dominicana*, but the former can be distinguished by the presence of a strong palatal tooth and a smooth to faintly toothed free columellar edge.

Occurrence.—Río Cana Section: Cercado Formation.

Distribution.—Upper Miocene, northern Dominican Republic.

Etymology.—Named after the Dominican Republic, the geographic region where fossils of *Neritina dominicana* occur.

Neritina jungi, new species

Text-fig. 11

Diagnosis.—Anterior set of columellar teeth composed of two medium and rounded teeth wider than

interspaces; median set composed of three large and rhomboid teeth wider than or equal to interspaces; posterior set composed of two to three rounded teeth wider than interspaces. Color pattern composed of parallel, interrupted axial lines marginating adapertural side of circular, elliptical, and unevenly distributed lunate open spots; pattern concentrated in two spiral bands, one below shoulder and other below midbody area, where shades of pigmentation interconnect axial lines.

Description.—Shell small, reaching 11.2 mm in height by 13.5 mm in width. Shell globose, thick, and opaque. Surface smooth with inconspicuous growth lines. Teleoconch with 2.0 whorls, excluding eroded apical whorls. Protoconch not preserved in type material. Spire low, suture impressed, sutural ramp inconspicuously concave, shoulder and body whorl rounded in cross section. Aperture lunate and large; outer lip thick, smooth inside, and rounded; parietal callus flat, thick, smooth, and abruptly expanding on its anterior half. Exhalant groove shallow, short, narrow, and transversely oriented. Columellar lip slightly concave, its free edge bearing three sets of teeth: anterior set composed of two medium and rounded teeth,



Text-figure 11.—*Neritina jungi*, new species. a: NMB H 18233 (Holotype), NMB locality 16843, Río Cana Section, ventral side, shell height 8.3 mm; b: NMB H 18234 (Paratype), NMB 16841, Río Cana Section, dorsal side, shell height 8.2 mm.

wider than interspaces; median set composed of three large and rhomboid teeth, wider than or equal to interspaces; posterior set composed of two to three rounded teeth, wider than interspaces.

Ground color grey-white overlain by brown-black, parallel, and interrupted axial lines, marginating adapertural side of circular, oval, and lunate open spots unevenly distributed over surface. Color pattern concentrated in two spiral bands, one immediately below shoulder and other below midbody area, where shades of pigmentation interconnect axial lines. Axial pattern is faded in midbody spiral band.

Type material.—Holotype NMB H 18233, measuring 8.3 mm in height by 9.7 mm in width. Paratype (1) UCMP No. 39948, measuring 8.2 mm in height by 9.7 mm in width (TU1378). Paratype (2) NMB H 18234 measuring 11.2 mm in height by 13.5 mm in width (NMB locality 16841).

Type locality.—NMB locality 16843, Río Cana Section, Cercado Formation, northern Dominican Republic.

Material.—*Neritina jungi* is presently known only from the three specimens: Río Cana section: NMB localities 16841 and 16843. Río Gurabo section: TU 1378.

Remarks and comparisons.—The grey-white background color overlain by brown-black parallel lines superficially resembles *Neritina figulopicta*. However, the large aperture, the absence of a large intermediate tooth, and the flat parietal callus readily distinguish *N. jungi* from *N. figulopicta*.

Occurrence.—(see APPENDIX): Río Cana section: NMB localities 16841 and 16843. Río Gurabo section: TU 1378.

Distribution.—Upper Miocene to lower Pliocene, northern Dominican Republic.

Etymology.—*Neritina jungi* is named in honor of Dr. Peter Jung for his extensive contributions to our knowledge of the systematics, biostratigraphy, and evolution of Caribbean molluscs.

Subfamily SMARAGDINAE Baker, 1923

Diagnosis.—Shell small (typically <1 cm high). Shell surface smooth and glossy, frequently with polymorphic color patterning on a green background pigment.

Remarks.—This subfamily comprises a single genus, *Smaragdia* Issel and subgenera *Smaragdia sensu stricto*, *Smaragdella* Baker, and *Smaragdista* Iredale. There are 13 described living species and four subspecies of *Smaragdia* and another ten names that have been proposed from Cenozoic fossil material. Unabia (1996) has reviewed the global distribution of *Smaragdia* and determined that it is pantropical, occurring

between 20°N and S latitudes. It is associated with seagrasses throughout this range and Unabia (1984) has documented that the Hawaiian species *S. bryanae* Pilsbry feeds directly upon leaf cell tissue of the seagrass *Halophila hawaiiiana* Doty and Stone by puncturing individual cells with the radula. A similar relationship has been observed in Moorea, French Polynesia, where *Smaragdia souverbiana* Montrouzier occurs on *Halophila decipiens* Ostenfield (Emmett & Hickman, unpub. data).

As a seagrass specialist, *Smaragdia* provides a proxy for the presence for seagrass beds in the fossil record (Costa *et al.*, 1998). Seagrasses generally are restricted to depths of less than 30 m and to low-energy settings of reduced water movement (McComb *et al.*, 1981). Some seagrasses are abundant in estuaries, where they are known to tolerate very low salinities (as little as 2 ppt for short periods) at times of high freshwater input or elevated salinities in estuarine situations of high evaporation and poor exchange with the ocean. In addition to its broad salinity tolerance, *Halophila* is exceptional in its ability to tolerate low light and turbid conditions, and it has been reported as deep as 85 m in very clear water. The bathymetric range of *Smaragdia*, however, does not necessarily extend as deep as the deepest seagrasses, and it is reasonable to expect that population densities peak in shallower water where seagrass beds are most extensively developed.

Justification for recognizing this clade as a higher taxon extends beyond shell and radular features to the unusual ecology of the constituent species and hypotheses implicating a separate evolutionary history of descent from a non-marine ancestor. This has been suggested by Unabia (1984) based on possible co-evolution of *Smaragdia* with the pre-marine progenitors of seagrasses. Non-marine ancestry also was suggested by Morton (1958), and, earlier, Bourne (1908) suggested freshwater ancestry.

Genus SMARAGDIA Issel, 1869

Type species.—*Nerita viridis* Linnaeus, 1758; subsequent designation Kobelt, 1879, p. 149. Florida, West Indies, Mediterranean.

Diagnosis.—Same as for subfamily.

Smaragdia viridis (Linnaeus, 1758)

Text-fig. 12

Nerita exiguus viridis Lister, 1685, pl. 601, fig. 18.

Nerita exiguus nigrolineus ore subcroceo Lister, 1685, pl. 605, fig. 31.

Nerita viridis Linnaeus, 1758, p. 778.

Nerita viridis Gmelin, 1791, p. 3679.

Neritina (*Smaragdia*) *viridemar* Maury, 1917, p. 152, pl. 24, fig. 11.

Neritina (Smaragdia) floridana Smith, 1937, p. 66, pl. 6, fig. 8.
Smaragdia viridis weyssei Russell, 1940, p. 257, pl. 46, figs. 5, 6.
Smaragdia viridis venezuelensis Weisbord, 1962, p. 116, pl. 8, figs. 14, 15.

Diagnosis.—Anterior set of columellar teeth composed of five or six teeth of medium size, wider than interspaces; median set composed of one large tooth; posterior set composed of three or four small teeth narrower than interspaces. Ground color bright green or beige, overlain by one of seven distinct patterns of black-brown lines described in detail below.

Description.—Shell small, reaching 6.9 mm in height by 7.5 mm in width, ovate to obliquely elongate, thin, opaque. Shell surface smooth, shiny, with microscopic growth lines. Teleoconch with 3.0 whorls. Protoconch papilliform, paucispiral with one and a half whorls, with a glossy white surface. Spire flat to slightly elevated, suture impressed, shoulder rounded to angulate, body whorl rounded in cross section. Aperture lunate, wider on anterior half; outer lip thin, smooth inside, flaring on anterior half; parietal callus convex, thick, shiny, smooth, expanded on its anterior half, with excavated triangular area near base; exhalant groove shallow, narrow, of medium length, and obliquely oriented in relation to shell axis. Columellar lip straight to slightly concave, free edge bearing 6 to 11 small teeth arranged in three sets. Anterior set composed of five or six teeth of medium size, wider than interspaces; median set composed of one large tooth; posterior set composed of three or four small teeth narrower than interspaces. In some specimens, third or posterior set of teeth either inconspicuous or absent, depending upon its growth stage.

Ground color beige or bright green; immaculate white specimens were observed by Parenzan (1970) in the Mediterranean. Seven distinct color patterns, from the total absence of color to a complex pattern of light to dark brown lines that are occasionally bordered by irregular white blotches, occur among specimens from the Dominican Republic. These color morph patterns are named and lettered as follows (Text-fig. 13):

Absent (A). Ground color without any trace of dark or light lines. Among the fossils we examined, about 12% were of pattern (A).

Restricted (R). Chevron axial lines are restricted to the shoulder area. Among the fossils we examined, about 40% were of pattern (R).

Interrupted (I). Wavy, axial lines extend from the shoulder to the base, but are interrupted in spiral sections. Among the fossils we examined, about 25% were of pattern (I).

Straight (S). Generally straight and solid axial lines extend from the suture or the shoulder to the base.

Among the fossils we examined, about 6% were of pattern (S).

Zigzag (Z). Zigzag lines extend from the shoulder to the base. Among the fossils we examined, about 12% were of pattern (Z).

Textile (T). Wavy broken axial lines are set either close to or apart from each other in alternate sections. These lines form polygonal open spaces between every two lines. Some areas have unevenly distributed broken lines. Among the fossils we examined, about 4% were of pattern (T).

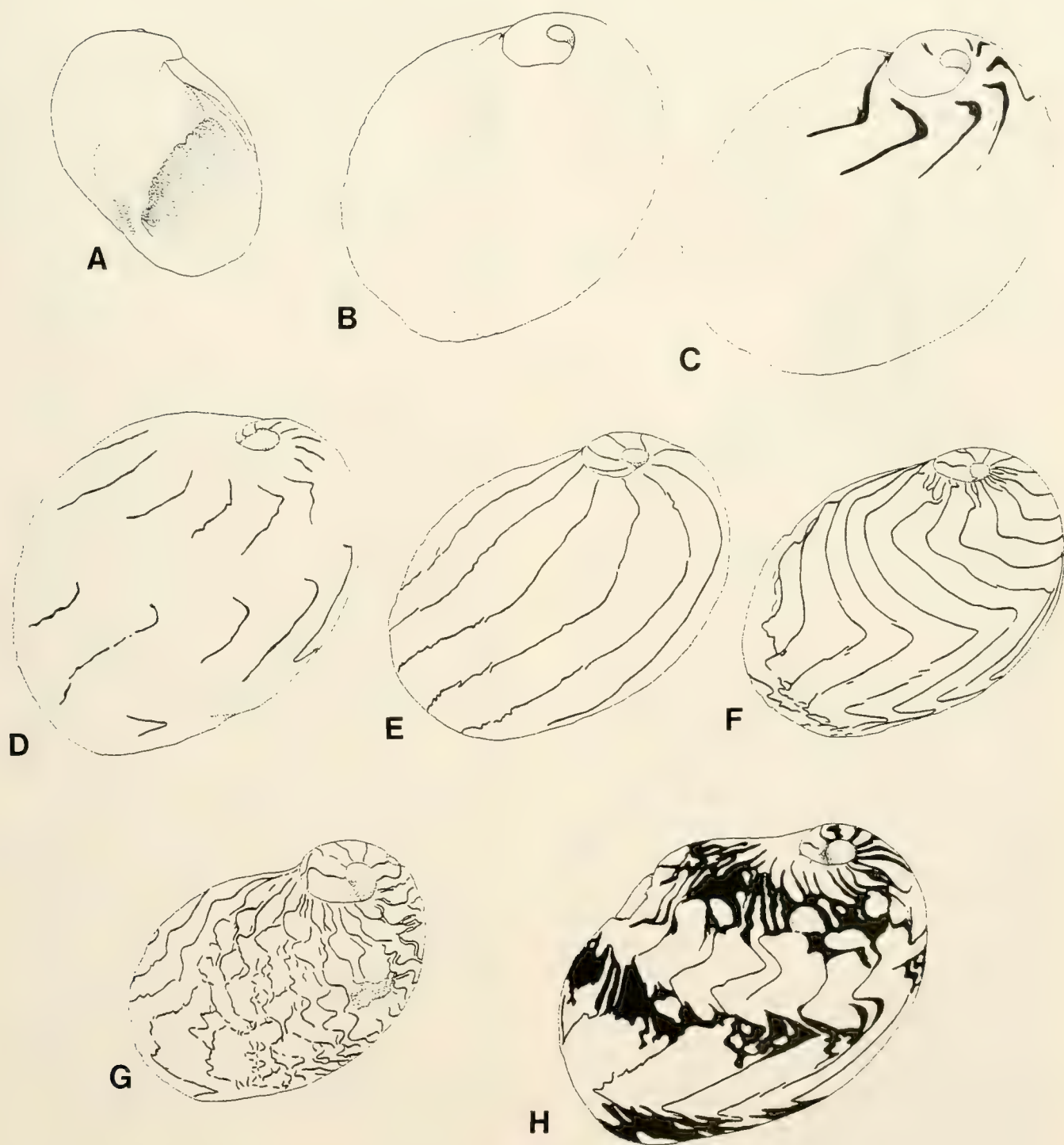
Banded (B). Narrow, zigzag axial lines are interconnected by wide axial flames arranged in three spiral bands: one at the shoulder, one at the midbody, and one at the base of the shell. Among the fossils we examined, about 1% of pattern (B). Pattern D has only been observed in Mediterranean specimens (Pope and Goto, 1991; Table 1).

Type material.—Linnaeus (1758), in his description of *Smaragdia viridis*, neither referred to a specimen in a collection nor to a figure that could be associated with the original material. Dance (1967) considered the type material of *S. viridis* to be lost. Kathie Way (personal communication, November 11, 1997), curator of the Linnean Zoological Collections, confirmed that the whereabouts of the type material of *S. viridis* is unknown. Thus, a Recent specimen, UCMP No. 39942, measuring 6.1 mm in height by 5.2 mm in width, is herein designated as the Neotype of *S. viridis*.

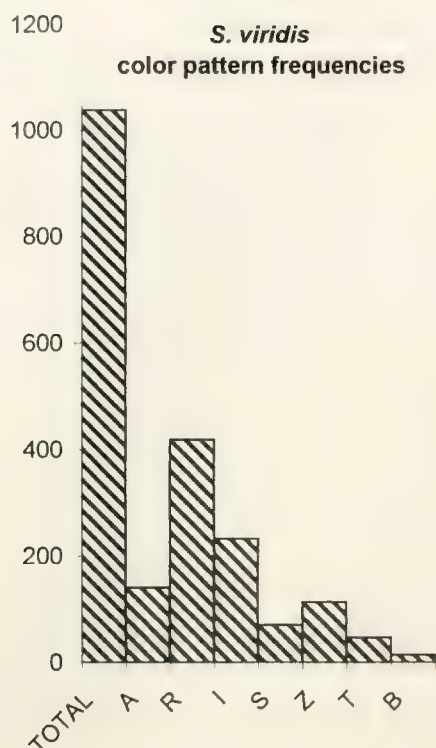
Type locality.—The type locality of *Smaragdia viridis* is herein designated as Cuba, Caribbean Sea, the site where the Neotype was collected (UCMP locality number 75).

Material.—More than 1000 fossil specimens are deposited in the collections of the Natural History Museum, Basel. Recent specimens from Florida, Panamá, Colombia, Venezuela, and Cuba, are in the Museum of Paleontology, University of California Berkeley, and specimens from the Mediterranean Sea are in F.H.A. Costa collection, Brazil.

Remarks and comparisons.—The first published record for *Smaragdia viridis* appeared in Lister (1685), where he named and illustrated two varieties, *Nerita exiguus viridis* from Barbados, and *N. exiguus nigro-lineus ore subcroceo* from Jamaica. The former variety has a solid tinted pattern, whereas the latter variety has wavy dark axial lines. The two names proposed by Lister (*op. cit.*) satisfy neither the Principle of Binomial Nomenclature of Article 5, nor the publication date after 1757 of Article 11, both Articles of the International Code of Zoological Nomenclature (1985).



Text-figure 12.—*Smaragdia viridis* (Linnaeus, 1758). a: TU 1294, Río Mao Section, ventral side, shell height 3.1 mm; b: TU 1294, Río Mao Section, dorsal side, pattern A (absent), shell height 4.3 mm; c: TU 1294, Río Mao Section, dorsal side, pattern R (restricted), shell height 4.6 mm; d: TU 1294, Río Mao Section, dorsal side, pattern I (interrupted), shell height 4.8 mm; e: NMB locality 16837, Río Cana Section, dorsal side, pattern S (straight), shell height 4.3 mm; f: NMB locality 16837, Río Cana Section, dorsal side, pattern Z (zigzag), shell height 4.1 mm; g: NMB locality 16837, Río Cana Section, dorsal side, pattern T (textile), shell height 4.0 mm; h: TU 1294, Río Mao Section, dorsal side, pattern B (banded), shell height 4.5 mm.



Text-figure 13.—Color morph frequencies for *Smaragdia viridis* (Linnaeus, 1758). See text and Text-figure 12 for descriptions of color morphs.

Thus, the two names proposed by Lister must be rejected.

Since the original description of *Smaragdia viridis* (Linnaeus, 1758), considerable disagreement has arisen regarding the identity of the Mediterranean and Caribbean populations of this species. Some workers accepted *S. viridis* as a single amphi-Atlantic and European species (Gmelin, 1791; Weinkauff, 1867; Gabb, 1872; Martens, 1879; Tryon, 1888; Pilsbry, 1922; Baker, 1923; Abbott, 1974; Nordsiek, 1982; Dance, 1990; Poppe and Goto, 1991; Barash and Danin, 1992; Rios, 1994; Unabia, 1996). Although Maury did not consider the Dominican fossil to be a subspecies of *S. viridis*, other authors have considered the Recent and fossil western Atlantic populations to be a subspecies of *S. viridis* (*S. viridis viridemaris* Maury, 1917); (Woodring, 1928; Warmke and Abbott, 1961; Scheltema, 1971; Jong and Coomans, 1988; Loch, 1994). A Recent population of *S. viridis* from the western Atlantic was also named as a subspecies (*S. viridis weyssei* Russell, 1940) based on color pattern differences between the Caribbean and European populations. Russell (1940) noted that the pattern of black lines is "... found in almost 100%..." of the European specimens, whereas the "... West Indian form never pos-

Table 1.—Character comparisons between Recent Mediterranean specimens and Caribbean fossils of *Smaragdia viridis*. Color morph abbreviations: A, absent; B, banded; D, diagonal; I, interrupted; R, restricted; S, straight; T, textile; Z, zigzag.

Character	Recent Mediterranean*	Neogene Dominican Republic
Shell shape	ovate to elongate	ovate to elongate
Spire	flat to elevated	flat to elevated
Shoulder	round to angulate	round to angulate
Ground color	white, beige, green	beige, green
Patterning**	A, I, S, Z, D	A, R, I, S, Z, T, B

* Parenzan, 1970; Poppe and Gotto, 1991.

** See text for descriptions.

sesses these solid black lines..." (Russell, 1940, 1941). *Smaragdia viridis venezuelensis* Weisbord, 1962 was described from the Pleistocene deposits of Venezuela and possesses a lower spire and a less rounded shoulder than its conspecific relatives.

Several morphological similarities among Recent Mediterranean, Recent Caribbean, and Neogene Caribbean specimens suggest that the Recent Mediterranean population, the Recent western Atlantic population, and the Neogene Dominican Republic fossils should not be placed in separate taxonomic categories (Table 1). There are also several non-morphological reasons that support the hypothesis that *S. viridis* is one amphi-Atlantic species: (1) Recent populations of *Smaragdia viridis* occur on oceanic islands such as Bermuda, Madeira, and Canary (Weinkauff, 1867; Martens, 1879; Baker, 1923; Barash and Danin, 1992); (2) *S. viridis* veligers have been collected in several samples across the Atlantic Ocean (Scheltema, 1971); (3) Gene flow in shallow-water benthic marine invertebrates has been documented between the eastern and western tropical Atlantic Ocean (Scheltema, 1966, 1968, 1971, 1992, 1995; Vermeij and Rosenberg, 1993); and (4) *Smaragdia* sp. have a pelagic phase that lasts from 55 to 110 days, which enhances their dispersal capability (Scheltema, 1971; Unabia, 1996).

Smaragdia merida (Dall, 1903) from the Pliocene Caloosahatche beds of Florida, is also considered to be a sub-species of *Smaragdia viridis* by some authors (Warmke and Abbott, 1961; Unabia, 1996). However, the former species is separated from the latter in having a smooth free edge of the columellar lip and a well-developed tooth projecting from the base of the columella.

Occurrence.—(see APPENDIX): Río Cana Section: NMB localities 16817, 16818, 16824, 16828, 16832, 16833, 16834, 16835, 16836, 16837, 16838, 16839, 16842, 16844, 16846, 16852, 16857, 16879, 16977, 16984, 16986, 16989, 16993, 16995, 17005, 17012, 17026.

Río Gurabo Section: TU 1297, 1379, NMB localities 15849, 15873, 15878, 15882, 15896, 15897, 15900, 15901, 15903, 15904, 15906, 15907, 15909, 15910, 15911, 15912, 15913, 15916.

Río Mao Section: TU 1294, NMB localities 16802, 16910, 16912, 16914, 16915, 16916, 16917, 16918, 16922, 16923, 16924, 16926, 16927, 16928, 16929, 16932, 17269.

Río Yaque del Norte Section: NMB localities 16935, 16936, 16938, 16942, 17265, 17273, 17286, 17287, 17288, 17289, 17290.

Distribution.—Miocene to Pliocene: northern Dominican Republic; Upper Pliocene: Bowden, Jamaica (Woodring, 1928), Costa Rica (Olsson, 1922); Playa

Grande, northern Venezuela (Weisbord, 1962); Pleistocene: Loxahatchee, Florida (Smith, 1937); Paris, France (Unabia, 1996); Palermo, Italy (Weinkauff, 1867). Recent: western Atlantic, from southeast Florida, United States, to Sao Paulo, Brazil, from the Gulf of Mexico to the West Indies and Bermuda (Russell, 1941; Scheltema, 1971; Abbott, 1974; Rios, 1994); eastern Atlantic, from the Straits of Gibraltar, Spain, to Senegal, Madeira and the Canary Islands (Weinkauff, 1867; Martens, 1879; Scheltema, 1971; Barash and Danin, 1992); Mediterranean, from the Straits of Gibraltar to Lebanon, from France to Tunisia, from the Adriatic Sea to Egypt (Weinkauff, 1867; Martens, 1879; Scheltema, 1971; Barash and Danin, 1992).

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APPENDIX

Samples used in this study.

Genus	Species	River	Sample	Meters	n
<i>Neritina</i>	<i>dominicana</i>	Cana	16850	228	2
<i>Neritina</i>	<i>figulopicta</i>	Cana	16856	165	5
<i>Neritina</i>	<i>figulopicta</i>	Cana	16855	172	1
<i>Neritina</i>	<i>figulopicta</i>	Cana	17003	175	1
<i>Neritina</i>	<i>figulopicta</i>	Cana	16841	228	35
<i>Neritina</i>	<i>figulopicta</i>	Cana	16842	228	1
<i>Neritina</i>	<i>figulopicta</i>	Cana	16843	228	21
<i>Neritina</i>	<i>figulopicta</i>	Cana	16844	228	2
<i>Neritina</i>	<i>figulopicta</i>	Cana	16846	228	6
<i>Neritina</i>	<i>figulopicta</i>	Cana	16848	228	15
<i>Neritina</i>	<i>figulopicta</i>	Cana	16850	228	3
<i>Neritina</i>	<i>figulopicta</i>	Cana	16851	228	5
<i>Neritina</i>	<i>figulopicta</i>	Cana	16988	228	2
<i>Neritina</i>	<i>figulopicta</i>	Cana	16838	233	3
<i>Neritina</i>	<i>figulopicta</i>	Cana	16835	252	1
<i>Neritina</i>	<i>figulopicta</i>	Cana	16872	685	1
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	16213	40	1
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15919	56	119
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	16204	56	11
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15920	58	44
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15918	60	31
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15916	90	1
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15915	100	1
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15912	105	1
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15911	111	2
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15910	119	1
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15903	121	4
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15900	123	1
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	15906	133	2
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	TU 1358	n/a	12
<i>Neritina</i>	<i>figulopicta</i>	Gurabo	TU 1378	n/a	2
<i>Neritina</i>	<i>figulopicta</i>	Mao	16917	n/a	1
<i>Neritina</i>	<i>figulopicta</i>	Mao	16923	n/a	1
<i>Neritina</i>	<i>figulopicta</i>	Mao	16926	n/a	1
<i>Neritina</i>	<i>figulopicta</i>	La barranca	17278	n/a	1
<i>Neritina</i>	<i>figulopicta</i>	Yaque	17283	13	1
<i>Neritina</i>	<i>figulopicta</i>	Yaque	17287	26	1
<i>Neritina</i>	<i>figulopicta</i>	Yaque	16943	49	1
<i>Neritina</i>	<i>jungi</i>	Cana	16841	228	1
<i>Neritina</i>	<i>jungi</i>	Cana	16843	228	1
<i>Neritina</i>	<i>jungi</i>	Gurabo	TU 1378	n/a	1
<i>Nerita</i>	<i>fulgurans</i>	Gurabo	15833		1
<i>Smaragdia</i>	<i>viridis</i>	Cana	17026	140	1
<i>Smaragdia</i>	<i>viridis</i>	Cana	17005	145	6
<i>Smaragdia</i>	<i>viridis</i>	Cana	16857	148	5
<i>Smaragdia</i>	<i>viridis</i>	Cana	16995	223	1
<i>Smaragdia</i>	<i>viridis</i>	Cana	16842	228	2
<i>Smaragdia</i>	<i>viridis</i>	Cana	16844	228	21
<i>Smaragdia</i>	<i>viridis</i>	Cana	16846	228	1
<i>Smaragdia</i>	<i>viridis</i>	Cana	16852	228	1
<i>Smaragdia</i>	<i>viridis</i>	Cana	16993	228	4
<i>Smaragdia</i>	<i>viridis</i>	Cana	16989	229	7
<i>Smaragdia</i>	<i>viridis</i>	Cana	16839	231	7
<i>Smaragdia</i>	<i>viridis</i>	Cana	16986	232	4
<i>Smaragdia</i>	<i>viridis</i>	Cana	16838	233	2
<i>Smaragdia</i>	<i>viridis</i>	Cana	16837	236	34
<i>Smaragdia</i>	<i>viridis</i>	Cana	16836	243	8
<i>Smaragdia</i>	<i>viridis</i>	Cana	16984	245	1
<i>Smaragdia</i>	<i>viridis</i>	Cana	16835	252	8

APPENDIX

Continued.

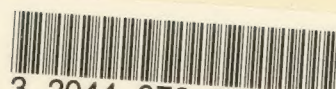
Genus	Species	River	Sample	Meters	n
<i>Smaragdia</i>	<i>viridis</i>	Cana	16834	280	17
<i>Smaragdia</i>	<i>viridis</i>	Cana	16977	300	3
<i>Smaragdia</i>	<i>viridis</i>	Cana	16828	310	13
<i>Smaragdia</i>	<i>viridis</i>	Cana	16824	320	2
<i>Smaragdia</i>	<i>viridis</i>	Cana	16879	343	2
<i>Smaragdia</i>	<i>viridis</i>	Cana	16817	345	6
<i>Smaragdia</i>	<i>viridis</i>	Cana	16818	346	6
<i>Smaragdia</i>	<i>viridis</i>	Cana	16832	385	4
<i>Smaragdia</i>	<i>viridis</i>	Cana	16833	385	5
<i>Smaragdia</i>	<i>viridis</i>	Cana	17012	458	1
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15916	90	2
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15913	103	1
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15912	105	5
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15911	111	2
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15909	112	1
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15910	119	23
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15903	121	39
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15900	123	29
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15901	123	3
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15907	127	30
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15904	127	45
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15906	133	31
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15897	136	16
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15896	136	10
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15882	186	4
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15878	195	25
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15873	206	24
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	15849	277	1
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	TU 1297	n/a	2
<i>Smaragdia</i>	<i>viridis</i>	Gurabo	TU 1379	n/a	46
<i>Smaragdia</i>	<i>viridis</i>	Mao	16802	n/a	6
<i>Smaragdia</i>	<i>viridis</i>	Mao	16910	n/a	4
<i>Smaragdia</i>	<i>viridis</i>	Mao	16912	n/a	1
<i>Smaragdia</i>	<i>viridis</i>	Mao	16914	n/a	6
<i>Smaragdia</i>	<i>viridis</i>	Mao	16915	n/a	2
<i>Smaragdia</i>	<i>viridis</i>	Mao	16916	n/a	4
<i>Smaragdia</i>	<i>viridis</i>	Mao	16917	n/a	3
<i>Smaragdia</i>	<i>viridis</i>	Mao	16918	n/a	9
<i>Smaragdia</i>	<i>viridis</i>	Mao	16922	n/a	6
<i>Smaragdia</i>	<i>viridis</i>	Mao	16923	n/a	4
<i>Smaragdia</i>	<i>viridis</i>	Mao	16924	n/a	3
<i>Smaragdia</i>	<i>viridis</i>	Mao	16926	n/a	28
<i>Smaragdia</i>	<i>viridis</i>	Mao	16927	n/a	8
<i>Smaragdia</i>	<i>viridis</i>	Mao	16928	n/a	18
<i>Smaragdia</i>	<i>viridis</i>	Mao	16929	n/a	15
<i>Smaragdia</i>	<i>viridis</i>	Mao	16932	n/a	15
<i>Smaragdia</i>	<i>viridis</i>	Mao	17269	n/a	2
<i>Smaragdia</i>	<i>viridis</i>	Mao	TU 1294	n/a	279
<i>Smaragdia</i>	<i>viridis</i>	Yaque	17286	22	22
<i>Smaragdia</i>	<i>viridis</i>	Yaque	17287	26	12
<i>Smaragdia</i>	<i>viridis</i>	Yaque	17288	29	17
<i>Smaragdia</i>	<i>viridis</i>	Yaque	17289	31	4
<i>Smaragdia</i>	<i>viridis</i>	Yaque	17290	33	20
<i>Smaragdia</i>	<i>viridis</i>	Yaque	16935	37	6
<i>Smaragdia</i>	<i>viridis</i>	Yaque	16936	41	7
<i>Smaragdia</i>	<i>viridis</i>	Yaque	17265	42	8
<i>Smaragdia</i>	<i>viridis</i>	Yaque	16938	45	10
<i>Smaragdia</i>	<i>viridis</i>	Yaque	16942	50	7
<i>Smaragdia</i>	<i>viridis</i>	La barranca	17273	n/a	1

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